A Comparative Bioenergetics Analysis of Seasonal Growth of Juvenile Sockeye Salmon and Their Consumption of Zooplankton in Great Central Lake and Sproat Lake, British Columbia, During 1999

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A COMPARATIVE BIOENERGETICS ANALYSIS OF SEASONAL GROWTH OF JUVENILE SOCKEYE SALMON AND THEIR CONSUMPTION OF ZOOPLANKTON IN GREAT CENTRAL LAKE AND SPROAT LAKE, BRITISH COLUMBIA, DURING 1999

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TABLE OF CONTENTS

LIST OF FIGURES	vi
LIST OF TABLES	vii
ABSTRACT and RÉSUMÉ	ix
INTRODUCTION	1
STUDY AREA AND SITE DESCRIPTION	2
METHODS	8
Temperature and oxygen	8
Water chemistry sampling	9
Zooplankton sampling	9
Zooplankton production calculations	9
Acoustic and trawl surveys (ATS)	10
Fish production and consumption analysis	10
RESULTS AND DISCUSSION GREAT CENTRAL LAKE	12
Temperature and oxygen	13
Water chemistry	13
Zooplankton average standing stock	13
Zooplankton seasonal trends	14
Zooplankton production	16
Sockeye salmon density, lengths, and weights	17
Juvenile sockeye diets	19
Nocturnal depth distribution of juvenile sockeye salmon	21
Juvenile sockeye bioenergetics and food consumption	23
RESULTS AND DISCUSSION SPROAT LAKE	29
Temperature and oxygen	30
Water chemistry	30
Zooplankton average standing stock	30
Zooplankton seasonal trends	32
Zooplankton production	33
Sockeye salmon density, lengths, and weights	34
Juvenile sockeye diets	34
Nocturnal depth distribution of juvenile sockeye salmon	36
Juvenile sockeye bioenergetics and food consumption	37
LITERATURE CITED	43
APPENDIX 1: ZOOPLANKTON DENSITY AND BIOMASS	48

LIST OF FIGURES

Figure 1	Location of Great Central, Sproat, and Henderson lakes on the west coast of Vancouver Island, B. C.	4
Figure 2	Great Central Lake bathymetry contours, acoustic and trawl transect lines, and sampling stations	5
Figure 3	Sproat Lake acoustic and trawl transect lines, and sampling stations	6
Figure 4	Sproat Lake bathymetric contours (in metres)	7
Figure 5	1999 GCL zooplankton density per L.	15
Figure 6	1999 GCL zooplankton biomass µg L^{-1} dry weight	16
Figure 7	Average zooplankton production in Great Central Lake 1999	17
Figure 8	Juvenile sockeye lengths with respect to time of year for GCL and Sproat Lake	19
Figure 9	Field measured average weights (± 95% CI) of juvenile sockeye salmon and average weights simulated using the bioenergetics model	24
Figure 10	Simulation 1 (minimum weights for dipterans): Bioenergetics-based estimates of GCL food consumption by juvenile sockeye salmon (g per ha wet weight per day) assuming that the fish feed in the top 30 m of lake water	25
Figure 11	Simulation 2 (maximum weights for dipterans): Bioenergetics-based estimates of GCL food consumption by juvenile sockeye salmon (g per ha wet weight per day) assuming that the fish feed in the top 30 m of lake water.	25
Figure 12	Sproat Lake 1999 zooplankton density per L	32
Figure 13	Sproat Lake 1999 zooplankton biomass µg L^{-1} dry weight	32
Figure 14	Average zooplankton production in Sproat Lake 1999	33
Figure 15	Sproat Lake field measured average weights (± 95% CI) of juvenile sockeye salmon and average weights simulated using the bioenergetics model	38
Figure 16	Bioenergetics-based estimates of Sproat Lake food consumption by juvenile sockeye salmon (g per ha wet weight per day) assuming that the fish fed between 5-30 m water depth	39

LIST OF TABLES

Table 1	Sample log for GCL and Sproat Lakes during 1999	8
Table 2	Great Central Lake oxygen and temperature profiles from1999	12
Table 3	GCL Nitrate (NO_3), Total Phosphorus (TP) and corrected Chlorophyll a (Chl a = total chlorophyll – phaeopigments) as µg per L	13
Table 4	Mean GCL1999 (June-November) zooplankton density, biomass, mean weights and egg densities.	14
Table 5	Average (3 June – 25 November) zooplankton standing stock, egg density, and production in GCL 1999.	17
Table 6	GCL acoustic and trawl based estimates of juvenile sockeye abundance	18
Table 7	GCL 1999 trawl-based juvenile sockeye lengths and weights	18
Table 8	Stomach contents of juvenile sockeye captured in GCL on five dates through the summer-fall of 1999	20
Table 9	Mean weights (µg dry weight) for crustacean zooplankton, chironomids, and dipterans (GCL)	21
Table 10	Nocturnal depth distribution (% of total) of juvenile sockeye salmon in GCL recorded on 09 August, 16 September, and 30 November	22
Table 11	Average 1999 GCL rates of consumption by juvenile sockeye salmon	27
Table 12	Percent of zooplankton standing stock and production consumed per day by juvenile sockeye	28
Table 13	Sproat Lake oxygen and temperature profiles	29
Table 14	Sproat Lake Nitrate (NO_3), Total Phosphorus (TP) and corrected Chlorophyll a (Chl a = total chlorophyll minus phaeopigments) as µg per L	30
Table 15	Mean Sproat Lake 1999 (June-November) zooplankton density, biomass, mean weight, and egg numbers	31
Table 16	Average 1999 Sproat Lake (8 June – 18 November) zooplankton standing stock, egg density, and production	33
Table 17	Sproat Lake acoustic and trawl based estimates of juvenile Sockeye abundance	34
Table 18	Sproat Lake 1999 trawl-based juvenile sockeye lengths and weights	34
Table 19	Mean weights (µg dry weight) for crustacean zooplankton, chironomids, and dipterans	35
Table 20	Rates of consumption of Sproat Lake prey by juvenile sockeye captured on four dates through the summer-fall of 1999	35
Table 21	Sproat Lake nocturnal depth distribution (% of total) of juvenile sockeye salmon	36

Table 22	Average 1999 Sproat Lake rates of consumption by juvenile sockeye salmon	40
Table 23	Percent of zooplankton standing stock and production consumed per day by Sproat Lake juvenile sockeye	41

APPENDIX 1

Table 1	Year 1999 Great Central Lake and Sproat Lake zooplankton (a) density (per L) and, (b) biomass (per L dry weight)	49

ABSTRACT

Hyatt, K.D., McQueen, D.J., Rankin, D.P., and Stockwell, M.M. 2016. A comparative bioenergetics analysis of seasonal growth of juvenile sockeye salmon and their consumption of zooplankton in Great Central Lake and Sproat Lake, British Columbia, during 1999. Can. Tech. Rep. Fish. Aquat. Sci. 3159: vii + 50 p.

Great Central Lake (GCL) and Sproat Lake are important Vancouver Island sockeye salmon nursery lakes. In most years since 1970, GCL has been treated with inorganic fertilizer additions and Sproat Lake has not. Our goal in 1999 was to estimate sockeye fry carrying capacity for both lakes. Our method was to compare consumption of zooplankton by juvenile sockeye with production by all of the zooplankton species observed in their diets. We found that GCL fry consumption averaged 130 g ha^{-1} d^{-1} wet weight (ww), which equalled 0.5% d^{-1} of prey standing stock and 8 to 81% d^{-1} of prey production. Sproat Lake fry consumed 400 g ha^{-1} d^{-1} ww in the spring declining through the summer-fall to < 100 g ha^{-1} d^{-1} ww, averaging 1.1% d^{-1} of prey standing stock and 2 to >100% d^{-1} of prey production. We conclude that in both lakes there was excess capacity for increased fry densities, and that the fall was the period when consumption by fish was most likely to exceed production by their zooplankton prey.

RÉSUMÉ

Hyatt, K.D., McQueen, D.J., Rankin, D.P. et Stockwell, M.M. 2016. Une analyse de la bioénergétique comparative de la croissance saisonnière du saumon rouge juvénile et leur consommation de zooplancton dans le Grand lac Central et Sproat Lake, Colombie-Britannique, en 1999. Rapp. tech. can. sci. halieut. aquat. 3159 : vii + 50 p.

Les lacs Great Central et Sproat sont d'importants lacs de séjour pour le saumon rouge sur l'île de Vancouver. Presque chaque année depuis 1970, GCL a été traitée avec des ajouts d'engrais inorganiques et Sproat Lake n'a pas. Notre objectif en 1999 était d'estimer la capacité biotique des deux lacs pour les alevins de saumon rouge. Notre méthode consiste à comparer la consommation de zooplancton par rouges juvéniles à la production de toutes les espèces de zooplancton observées dans leur alimentation. Nous avons constaté que la consommation moyenne des alevins du lac Great Central était de 130 g à l'ha-1 d-1 poids humide (ph), ce qui équivalait à 0,5 % d-1 du stock actuel de proies et à 8 à 81 % d-1 de la production de proies. Les alevins du Lac Sproat, quant à eux, avaient consommé 400 g à l'ha-1 d-1 ph au printemps, chiffre qui avait décliné à l'été et à l'automne pour atteindre < 100 g à l'ha-1 d-1 ph, soit une moyenne de 1,1 % d-1 du stock actuel de proies et de 2 à 100 % d-1de la production de proies. Nous avons conclu à une capacité excédentaire pour l'augmentation de la densité des alevins dans les deux lacs, et noté que l'automne était la période pendant laquelle la consommation des poissons était la plus susceptible de dépasser la production de leurs espèces proies de zooplancton.

INTRODUCTION

The carrying capacity of sockeye salmon "nursery" lakes has been operationally defined as the point at which the maximum sustainable number and biomass of smolts are produced (Shortreed et al. 2000). The latter information is important in salmon management because it may be used as a basis for identifying desirable escapement and spring fry recruitment targets to maximize smolt yield in a given lake. The objective of our investigations in 1999 at Great Central Lake (GCL) and Sproat Lake was to employ bioenergetics analysis to estimate zooplankton consumption by fish relative to zooplankton standing crop and production in order to expand our understanding of how between-lake differences in food-web structure and function might influence the carrying capacity of selected nursery lakes for sockeye salmon (*Oncorhynchus nerka)*.

Carrying capacity has been estimated for a number of British Columbia sockeye salmon nursery lakes using the photosynthetic rate model (PRM) (Hume et al. 2003, Shortreed et al. 2000, 2001). The PR model is a modification of the epilimnetic volume model (EVM) (Koenings and Burkett 1987) which was developed for Alaskan lakes where abiotic factors such as glacial silt and organic stain varied widely but nutrient loading varied relatively little. In Alaskan lakes euphotic zone volume was used as an analogue for areal primary production and was correlated with juvenile sockeye salmon production. Hume et al. (2003) showed that British Columbia sockeye nursery lakes had a greater range in nutrient loading than Alaskan Lakes, and biotic factors (phytoplankton biomass and productivity) were important enough in determining euphotic zone depth to seriously limit the utility of EVM projections of BC nursery lake carrying capacities.

To remedy problems encountered in applying the EVM to BC nursery lakes, Hume et al. (2003) developed the photosynthetic rate model (PRM) which is based on a correlation between photosynthetic rate expressed as metric tons of carbon per year and associated maximum production of sockeye smolt biomass (Shortreed et al, 2000). The empirically-based PRM has emerged as a promising tool to establish first order approximations of logarithmic-scale, carrying-capacity differences for juvenile sockeye among lakes exhibiting PRs varying by more than an order of magnitude and practical applications of the PRM are found in Shortreed et al. (2000, 2001) and Cox-Rogers et al. (2004).

Shortreed et al. (2000) noted, that there are several assumptions that potentially limit the utility of the PRM, and these authors also recommended testing its applicability in a wider range of lakes. The PRM assumes that all primary production is equally likely to stimulate zooplankton production and therefore enhance food availability for juvenile sockeye salmon. Differences in phytoplankton and zooplankton species composition are implicitly assumed to be unimportant to fish production outcomes. Thus, contrary to a voluminous literature on lacustrine food-webs, largely inedible blue-green algae are assumed to stimulate as much zooplankton production as optimally sized, highly-edible, green algae. Similarly, evasive and difficult to catch copepods (Hyatt 1980) are

assumed to be an energetically equivalent food source to slow moving and easily captured, large-bodied, cladocerans for planktivorous fish.

Our current work, involving a food-web based approach to these issues (Hyatt et al. 2005, McQueen et al. 2007), began with the 1999 Great Central and Sproat Lake data collection described here. Our goal was to collect a relatively detailed data set that would allow us to apply bioenergetics-based, production and consumption analysis to the determination of lake-specific, carrying capacities for production of juvenile sockeye salmon (Beauchamp et al. 1989, Chipps and Bennett 2000, Beauchamp et al. 2004, Hyatt et al. 2005, McQueen et al. 2007). Our protocol was to estimate species-specific production rates for all major zooplankton species and age-specific growth, survival and seasonal diets for juvenile sockeye. We then calculated consumption by sockeye of each of the major zooplankton taxa and compared daily zooplankton production and standing stock with daily rates of consumption by sockeye. From this we directly assessed the impacts of juvenile sockeye on their food sources, estimated rates of exploitation competition and made inferences about the impacts of available food on sockeye growth rates. Multi-year observations from a companion report (Hyatt et al. 2016) are anticipated for use along with the bioenergetics modelling procedures developed here to characterize the average carrying capacity of each of the three Barkley Sound nursery lakes to support their respective pelagic fish populations.

STUDY AREA AND SITE DESCRIPTION

Great Central and Sproat lakes lie within the western area of the Somass Watershed which drains an area of about 1,426 km² into Alberni Inlet, a 54.3 x 1.5 km coastal fjord on southwestern Vancouver Island (Figure 1; Morris & Leaney 1981). The Somass Watershed consists of three major sub-basins: the Sproat system (387.5 km² in area), dominated by Sproat Lake, which drains into the Sproat River (mean daily flow 37.9 m^3/s); the Great Central Lake system (651 km²), which drains into the Stamp River (mean daily flow 58.9 m^3/s); and the Ash system (388 km²), draining Oshinow and Elsie lakes (mean daily flow 16.7 m^3/s) into the Stamp, which flows 15 km into the Somass River (Manzer, Morley, and Girodat 1985). The Somass River (mean daily flow rate of 121.4 m^3/s) runs for 8 km to its mouth at the head of Alberni Inlet.

The watersheds that contain Great Central and Sproat lakes experience a marine west coast climate, designated *Cfb* in the Koppen classification system (Peel, Finlayson, and McMahon, 2007), characterized by mild winters, warm summers, no dry season, and long spring and autumn seasons with small seasonal ranges in temperature. The climate is distinguished by several factors: the mean temperature ranges between 0°C and 22°C; and on average even the driest month of the year receives more than 30 mm of precipitation. In general, the climate in the northeastern Pacific also undergoes multi-decadal changes which affect climate variables such as air temperature and precipitation that fluctuate with the *Pacific Decadal Oscillation* index[1] (Hare and Mantua 2000) in these watersheds.

[1] The Pacific Decadal Oscillation (PDO) is a pattern of Pacific climate variability that shifts phases on at

Great Central and Sproat lakes both serve as nursery lakes for juvenile sockeye salmon production that ultimately supports a valuable mixed stock fishery for sockeye salmon in Barkley Sound (Hyatt and Steer 1987). Given their geographic proximity, the three lakes exhibit sufficiently similar geology, climatology, hydrology and nutrient dynamics to be classified as highly unproductive, oligotrophic, lakes typical of the British Columbia outer coast (Stockner and Shortreed 1985, Hyatt et al. 2004). Specific characteristics of each lake (Shortreed, et al. 2001) are as follows: Great Central Lake (lat. 49°22' long. 125°15'lat., elevation 82 m), surface area 5100 ha, mean depth 212 m, water residence time 7.3 y, average total phosphorus TP = 2.6 μg L^{-1}); Sproat Lake (lat. 49°14' long. 125°06' lat., elevation 29 m, surface area 4100 ha, water residence time 8.0 y, mean depth 59 m, average TP = 2.7 μg L^{-1}). The lakes undergo one period of thermal stratification and one thermal mixing cycle each year (i.e. are monomictic), usually in the fall.

Both lakes have long histories of intentional manipulations (Hyatt and Steer 1987) including lake fertilization (at Great Central Lake 1970-1973, 1977-present; Henderson Lake 1976-1997, 1999, 2007; Sproat Lake 1985) and variable recruitment of sockeye fry associated with fluctuations in both adult returns and fisheries management objectives (all lakes; Dobson et al. 2005).

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least inter-decadal time scale, usually about 20 to 30 years. The PDO is detected as warm or cool surface waters in the Pacific Ocean, north of 20° N. During a "warm", or "positive", phase, the west Pacific becomes cool and part of the eastern ocean warms; during a "cool" or "negative" phase, the opposite pattern occurs (Hare and Mantua 2000).

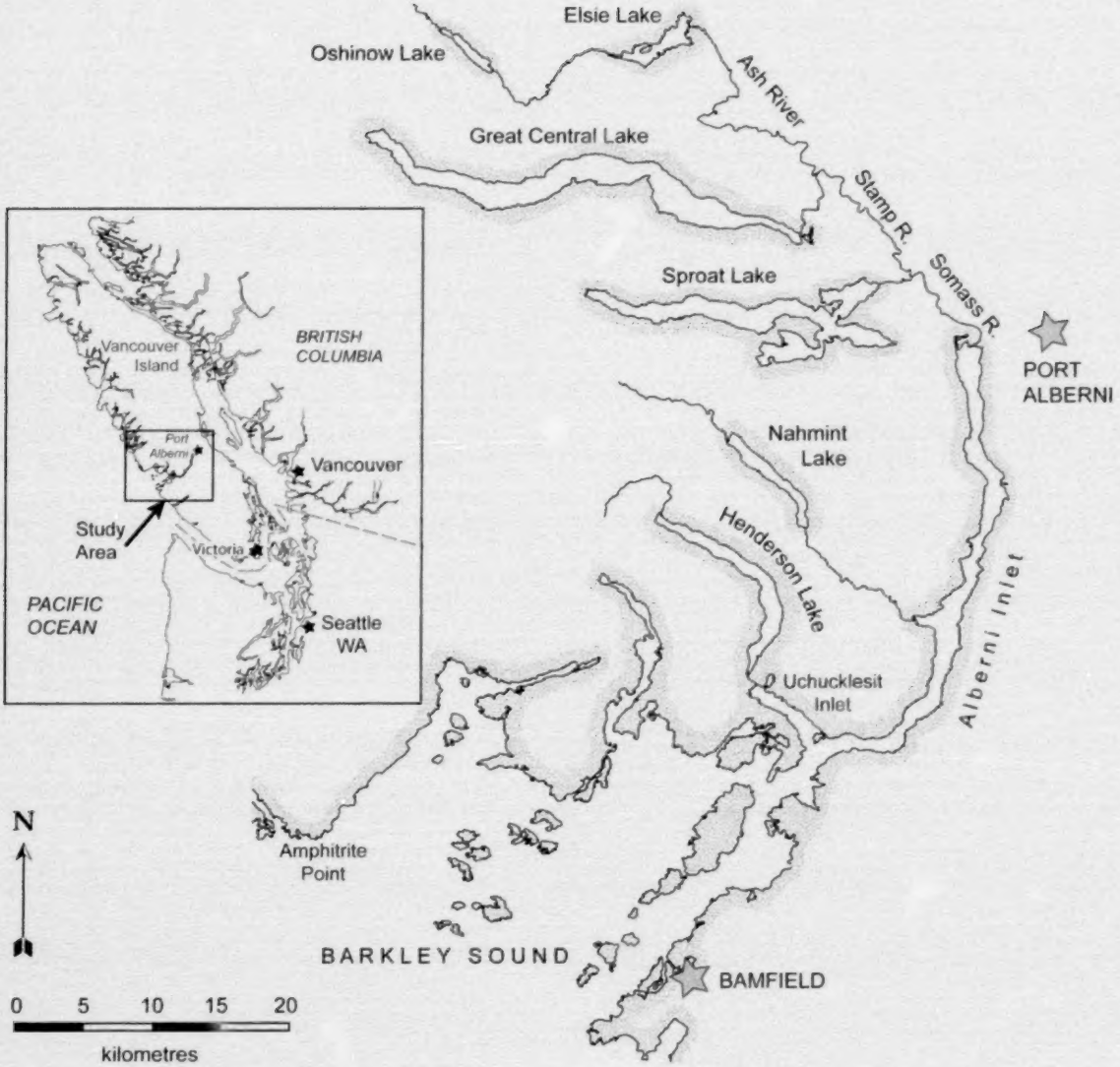

Figure 1. Location of Great Central, Sproat, and Henderson lakes on the west coast of Vancouver Island, B. C.

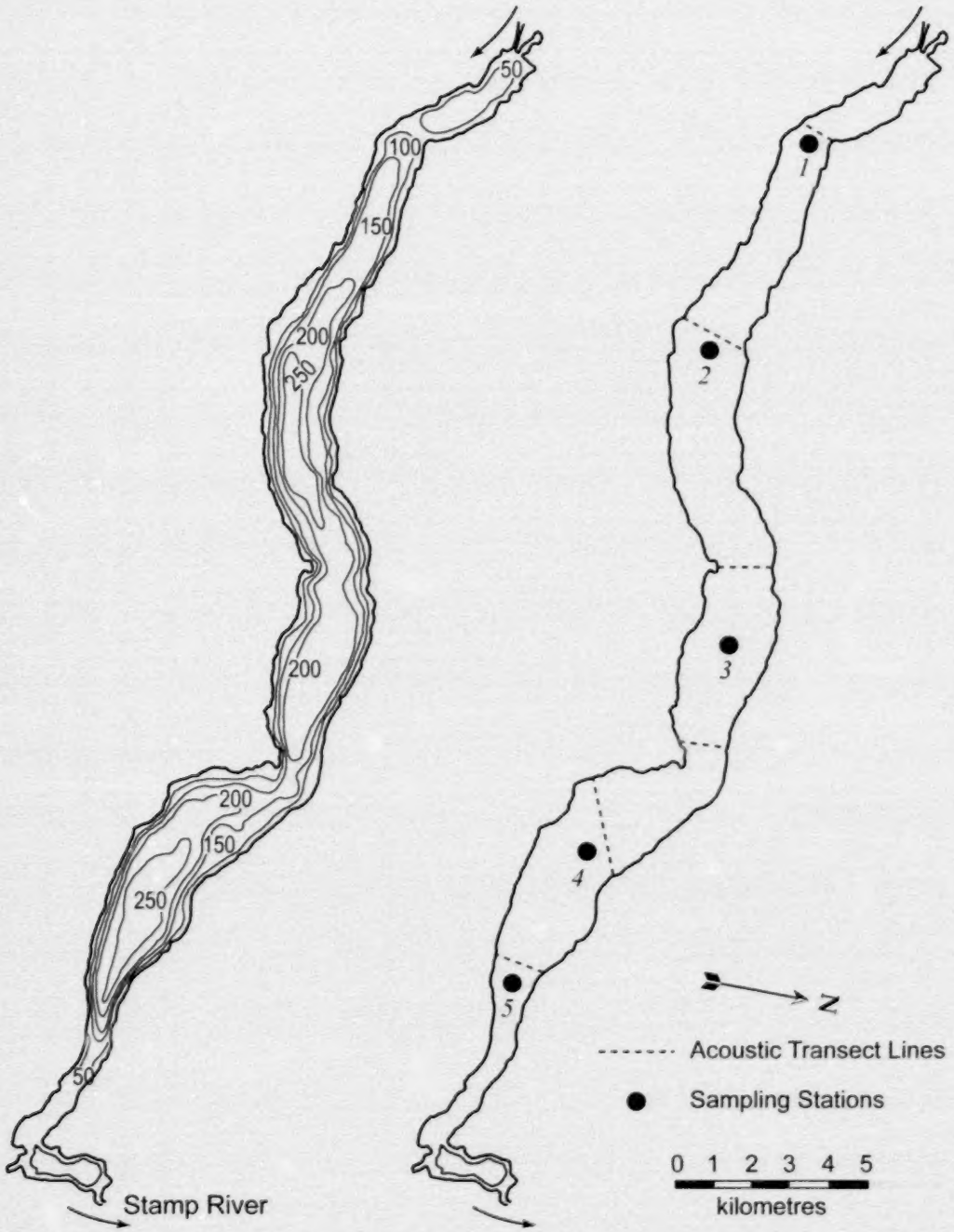

Figure 2. Great Central Lake (a) bathymetry contours (in metres) and (b) acoustic and trawl transect lines, and sampling stations. Zooplankton samples were collected at all stations and water chemistry samples were collected from stations 2 and 3. Maps adapted from Rutherford et al. 1986.

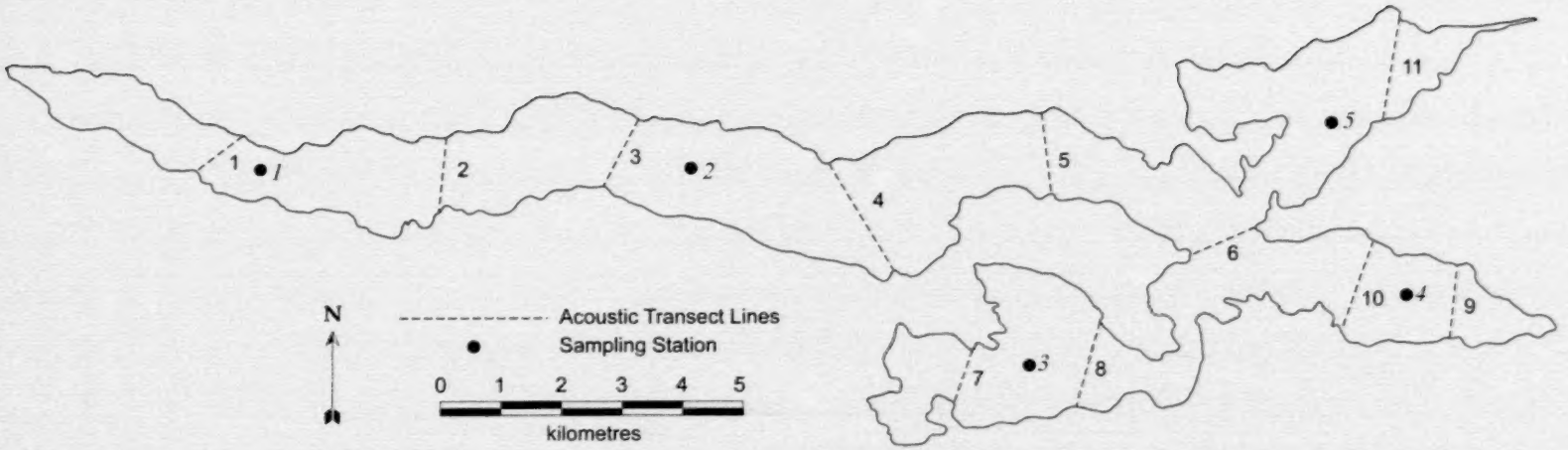

Figure 3. Sproat Lake acoustic and trawl transect lines, and sampling stations. Zooplankton samples were collected at all stations and water chemistry samples were collected from stations 2 and 3. Maps adapted from Rutherford et al. 1986.

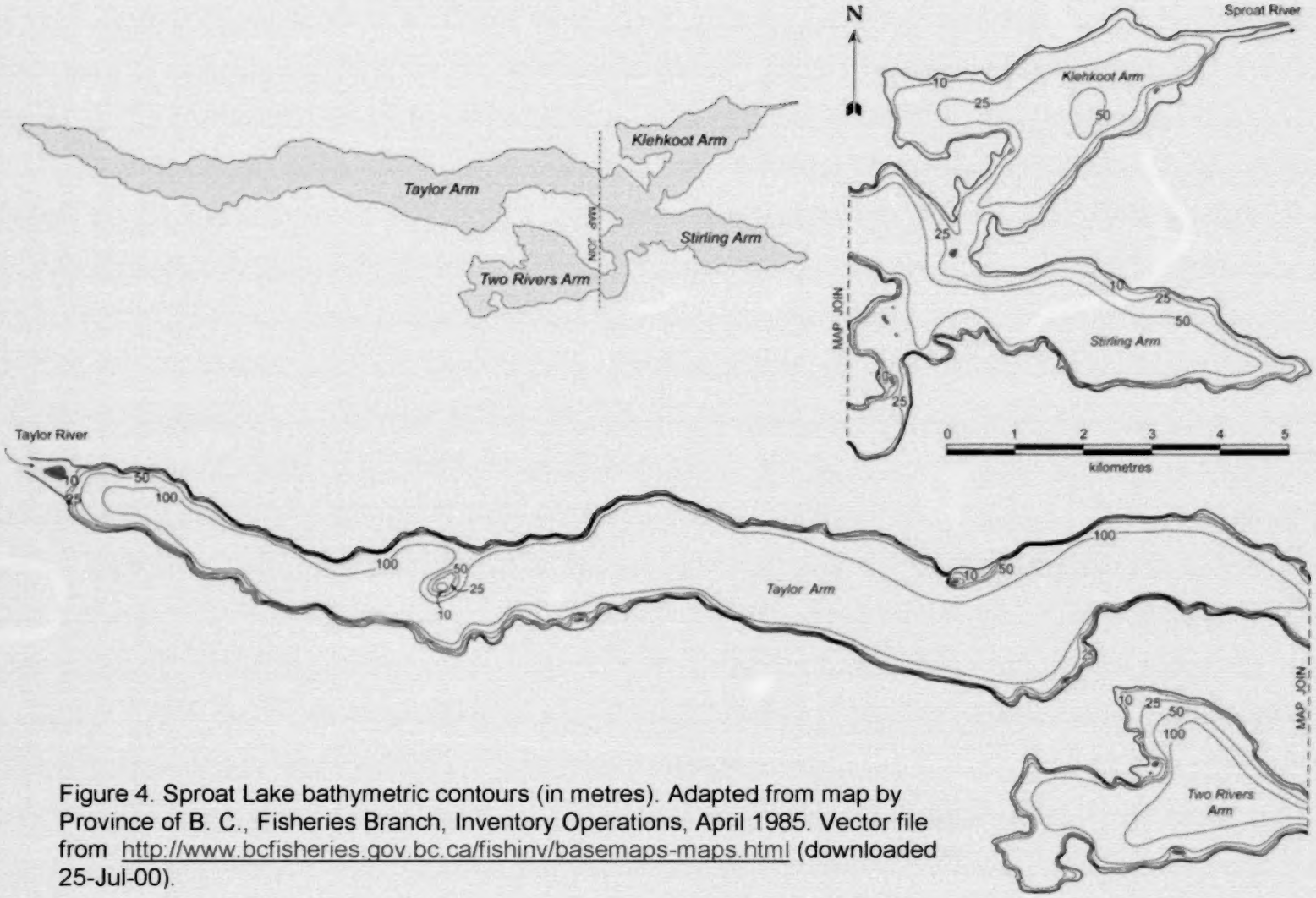

Figure 4. Sproat Lake bathymetric contours (in metres). Adapted from map by Province of B. C., Fisheries Branch, Inventory Operations, April 1985. Vector file from http://www.bcfisheries.gov.bc.ca/fishinv/basemaps-maps.html (downloaded 25-Jul-00).

METHODS

Physical, chemical, and biological data were collected in both lakes from June-December 1999 (Table 1).

Table 1. Sample log for GCL and Sproat Lakes during 1999.

Date	Oxygen	Temperature	Chemistry	Secchi depth	Zooplankton	Sockeye fry length-weight	Sockeye fry abundance	Fry diel distribution
GREAT CENTRAL LAKE								
03-Jun-99		x			x			
21-Jun-99	x	x	x		x	x	x	
12-Jul-99	x	x	x		x			
21-Jul-99		x	x	x	x		x	
02-Aug-99	x	x	x	x	x	x		x
21-Aug-99	x	x	x	x	x			
13-Sep-99	x	x	x	x	x			
16-Sep-99						x		x
26-Oct-99		x	x		x			
25-Nov-99			x		x			
29-Nov-99	x	x				x	x	x
SPROAT LAKE								
08-Jun-99	x	x			x			
27-Jun-99	x	x	x		x	x	x	
19-Jul-99	x	x		x	x	x	x	
03-Aug-99	x	x	x		x	x		x
30-Aug-99			x		x			
20-Sep-99			x		x			
25-Oct-99			x		x			
30-Nov-99	x	x	x			x	x	x

TEMPERATURE AND OXYGEN SAMPLING

A YSI temperature-oxygen meter was employed to obtain vertical profiles of temperature and oxygen on 4-7 dates at one meter intervals from surface to 30m in each of GCL and Sproat lakes (Figures 2 and 3) during surveys extending from spring (June 3rd) to fall (November 29th) of 1999.

WATER CHEMISTRY SAMPLING

Limnological samples were collected at 1, 3, 5 m (epilimnion) and 20 m (hypolimnion) at each of two stations on each lake (Great Central at stations 2 and 4; Sproat at stations 2 and 3; Figures 2 and 3). Total phosphorus (TP) samples were stored in screw-cap test-tubes in the dark until analysis. $NO_3 + NO_2$ samples were passed through an acrodisk filter, placed in screw-cap plastic bottles, and frozen until analysis. Chlorophyll a samples were filtered (47 µm Millipore) and frozen until analysis. Samples were analyzed at the Cultus Lake laboratory, Fisheries and Oceans Canada.

ZOOPLANKTON SAMPLING

Zooplankton samples were collected every 3-4 weeks spring to fall at each of five stations (Figures 2 and 3) on each lake. Samples were collected at night using a metered (Rigosha and Co., Ltd. Model 5571) vertical haul net (square mouth, 30 x 30 cm) (Filion 1991) winched at 1 m s^{-1} between 25-0 m. Two mesh sizes (100 µm and 250 µm) were used. Samples were placed in individual sample jars, preserved in 4% buffered and sugared formalin and returned to the laboratory. For each sample, Rigosha meter values were used to calculate net filtration efficiency. For each date, a composite zooplankton sample was created from the five samples taken from each lake. The composite comprised zooplankton found in equal volumes of lake water taken from each of the four stations. These combined samples were identified to species for Cladocera, copepod adults, copepodids, and to suborder for nauplii. Eggs were counted for all species. To calculate biomass, body lengths of all animals were measured using a semi-automated counting and measuring system (Allen et al. 1994). Corrections for contraction due to preservation were applied to the body length of *Holopedium gibberum* (Yan and Mackie 1987), but not to other species (Campbell and Chow-Fraser 1995). Animal weights were estimated using length-weight regressions summarized in Girard & Reid (1990). If preserved animals were used to develop these regressions, a correction for weight loss in formalin was applied (Giguère et al. 1989).

ZOOPLANKTON PRODUCTION CALCULATIONS

Species-specific zooplankton production rates were calculated using the methods of Borgmann et al. (1984). Egg development time was based on the Belehrádek equation $K=a(T-\alpha)^b$ where T is temperature and a, α, and b are constants (Cooley et al. 1986). Production was calculated as $P = (N_{t+1}-N_t)(b/r)w$. Instantaneous birth rate was calculated following Paloheimo (1974). Instantaneous rate of population change was calculated as in Cooley et al. (1986), summarized in McQueen et al. (2007). For each species, on a sample by sample basis, we compared the potential biomass increase calculated using the production model with the actual biomass increase observed in the field, and in all cases we selected the larger of the two (McQueen et al. 2007).

ACOUSTIC AND TRAWL SURVEYS (ATS)

Juvenile sockeye salmon densities were estimated at night by using a Simrad EYM 70 KHz sounder deployed over whole-lake transects (GCL = 6 transects, Sproat Lake = 11 transects) and several depth strata (Figures 2, 3, and 4). Density estimates were used to determine total numbers of juvenile sockeye salmon found in each lake and these data were used to estimate sockeye salmon mortality throughout the late summer, fall and winter periods. Fish bio-samples were collected using a mid-water trawl net (2 m x 2 m mouth opening x 7.5 m long, Gjernes 1979). Haul depths were selected on the basis of simultaneous acoustics survey results used to identify depth-strata containing targets of interest. Detailed methods for our acoustics-and-trawl based surveys (ATS) of pelagic fish are described in Hyatt et al. (1984) and McQueen et al. (2014).

Samples of trawl-caught fish were returned to the laboratory for subsequent length, weight and age determinations. Juvenile fish destined for stomach-content analysis were placed into 90% ethanol immediately upon capture. Prior to analysis, stomachs were removed, contents washed into a petri dish and all prey items, which consisted principally of zooplankton, were counted. Stomach content data were used to estimate the numbers of each prey species consumed by sockeye salmon and these data were used to parameterize the fish bioenergetics model (described below). Because many of the prey had been damaged during consumption, we estimated individual prey weights from the average weights of each prey species-type found in the zooplankton samples collected on each sampling date. This method had little influence on modelled consumption rates, but since it is likely that the fish selected the largest prey available, translations of modelled biomass estimates into numbers of prey consumed, may have resulted in over-estimates of numbers of prey consumed (i.e. fewer larger prey account for the same biomass as more smaller prey).

FISH PRODUCTION AND CONSUMPTION ANALYSIS

The goal of this analysis was to calculate consumption by the fish as a percentage of production by each zooplankton prey species-type. When consumption of zooplankton by fish exceeded zooplankton production, we expected to see the zooplankton population decline, and at that point, we could assume that the "sockeye salmon production capacity" of the lake had been reached or exceeded on one or more dates.

Calculated rates of zooplankton consumption by age-0 sockeye salmon were based on the bioenergetics model (Kitchell et al. 1974, 1977) summarized in Hanson et al. (1997). Bioenergetics simulations of sockeye fry life-history intervals were based on observations beginning in June and ending in late November. Model inputs included diel changes in fish distributions within the water column, average temperatures of water used by most fish, fish lengths, weights and diets. Energy densities for the sockeye salmon and the various prey species were entered as joules/g wet weight and were set by the model at 5233 J/g for sockeye, 2500 J/g for copepods, 3000 J/g for cladocerans, 2500 J/g for chironomids and adult dipterans 2000 J/g for adult dipterans. Because Levy (1990) identified a variety of diel migration patterns exhibited by juvenile sockeye

salmon in BC lakes, we assessed diel vertical migration activity on three dates in GCL and two dates in Sproat Lake (dates in Table 1). We used these data to identify lake-specific vertical migration patterns and to establish mean temperatures experienced by sockeye during typical diel intervals.

Many of our conclusions are based on the assumption that the bioenergetics-based production and consumption values accurately reflect independent estimates obtained by other means. Several published comparisons from empirical studies suggested good agreement with energetics model estimates: (1) Under laboratory conditions, Brett et al. (1969) and Brett and Blackburn (1981) measured the growth rates of juvenile sockeye with respect to temperature, oxygen concentrations and food availability. For small sockeye (5 g) they found that maximum growth rates were 1.4 % of body weight gained per day. For age-0 sockeye feeding in the wild (current work) the average weight gain was 1.32% per day for GCL and 0.79 for Sproat Lake. (2) In the experiments noted above, Brett et al. (1969) showed that maximum growth rates for juvenile sockeye were obtained when daily ration equalled 6 % of body weight per day. For wild sockeye feeding in GCL and Sproat Lake, the model predicted that the fish consumed 5.9 and 6.7% body weight per day respectively. From this we conclude that the growth and consumption rates predicted by the model are about what we would expect based on general knowledge of sockeye metabolism. (3) Bevelhimer and Adams (1993) used a bio-energetic model to simulate diel vertical migration by kokanee and found that they consumed 4.5% body weight per day and grew at a rate of about 1% body weight per day. These are similar to the rates observed in our study.

RESULTS AND DISCUSSION GREAT CENTRAL LAKE

Table 2. Great Central Lake oxygen and temperature profiles from 1999. The dark area represents temperatures >17^{O} C which are usually avoided by juvenile sockeye salmon.

	Temperature (^{O} C)							Oxygen (mg L^{-1})			
Depth	03-Jun-99	21-Jun-99	12-Jul-99	02-Aug-99	21-Aug-99	13-Sep-99	29-Nov-99	03-Jun-99	21-Jun-99	13-Sep-99	29-Nov-99
0	14.6	15.3	21.3	22.3	19.6	19.1	6.8	8.0	10.1	9.0	10.4
1	14.4	15.2	20.3	21.4	19.5	19.0	7.0	8.2	10.4	9.0	10.3
2	14.1	14.7	19.4	20.8	19.4	19.0	7.0	8.6	10.5	9.0	10.3
3	13.6	14.6	19.0	20.4	19.4	18.9	7.0	8.9	10.5	9.0	10.3
4	13.2	14.3	18.4	20.1	19.3	18.9	6.8	9.0	10.5	9.0	10.3
5	13.0	14.1	16.8	19.5	19.3	18.8	7.0	9.0	10.6	9.0	10.3
6	12.9	13.9	14.9	18.9	18.9	18.3	7.0	9.1	10.6	9.0	10.3
7	12.8	13.3	13.3	17.5	18.3	16.7	7.0	9.0	10.6	9.5	10.3
8	11.4	12.0	11.7	15.6	17.1	15.7	7.0	9.3	10.6	10.3	10.3
9	10.1	10.7	10.1	14.3	14.2	15.3	7.0	9.7	11.1	10.7	10.3
10	9.8	9.0	9.4	13.1	12.7	14.2	6.8	9.7	11.3	10.9	10.3
11	9.1	9.4	8.9	12.2	11.2	12.0	6.9	9.5	11.2	11.2	10.3
12	8.2	7.9	8.5	11.5	10.2	10.8	7.0	9.7	11.4	11.5	10.3
13	7.7	7.6	8.2	10.4	9.2	10.0	6.9	9.9	11.3	11.6	10.3
14	7.3	7.4	7.4	9.8	8.0	9.3	6.9	9.9	11.3	11.6	10.3
15	6.6	7.0	7.2	9.2	7.3	8.6	6.9	10.0	11.3	11.6	10.3
16	6.2	6.9	6.9	8.5	6.9	8.4	7.5	10.0	11.3	10.6	
17	6.0	6.7	6.6	7.8	6.6	7.5	6.9	9.9	11.1	11.5	10.3
18	5.5	6.4	6.5	7.5	6.4	7.0	6.7	10.2	11.1	11.3	10.3
19	5.3	6.2	6.4	7.2	6.1	6.6	6.9	10.2	11.0	11.0	10.3
20	5.2	6.0	6.2	7.0	5.9	6.3	6.8	10.1	10.9	10.9	10.3
21	5.1	5.8	5.8	6.6	5.7	5.9	6.6	10.6	10.9	10.8	10.3
22	5.1	5.7	5.7	6.3	5.3	5.8	7.4	10.0	10.8	10.7	
23	5.0	5.6	5.5	6.2	5.2		7.2	10.0	10.7		
24	5.0	5.5	5.4	6.0	5.1	5.8	7.2	9.9	10.7	10.6	
25	4.9	5.4	5.3	5.8	5.0	5.6	7.2	9.9	10.6	10.5	
26	4.9	5.3	5.3	5.6	4.9		7.0	9.8	10.6		
27	4.8	5.3	5.3	5.4	4.8		6.8	9.8	10.6		
28	4.7	5.2	5.2	5.3	4.7		6.2	9.7	10.5		
29	4.8	5.2	5.2	5.2	4.7		6.0	8.2	10.6		
30		5.2			4.6				10.5		

TEMPERATURE AND OXYGEN

The GCL thermocline formed in early summer at 10-13 m. Epilimnial water warmer than 17^{O} C extended from the surface down to approximately 8 m depth (Table 2). Temperatures warmer than 17^{O} C have been associated with negative growth (Brett et al. 1969) and are often avoided by juvenile sockeye salmon (Levy 1990, 1991).

WATER CHEMISTRY

GCL macro-nutrient concentrations were low classifying it as oligotrophic (Table 3). Nitrate concentrations declined rapidly through the season and then increased during fall turnover. Total phosphorus (TP) comprising all phosphorus including the contents of algal cells remained constant through the season. Chlorophyll a concentrations remained stable through the summer. This suggests that algal cells were grazed and senesced as quickly as they were produced.

Table 3. Nitrate (NO_3), Total Phosphorus (TP) and corrected Chlorophyll a (Chl a = total chlorophyll – phaeopigments) as µg per L.

	Epilimnion			Hypolimnion	
Date	NO_3	TP	Corrected Chl a	NO_3	TP
23-Jun-99	22.6	3.9	0.7	32.1	3.4
13-Jul-99	4.4	3.5	0.5	31.5	3.3
03-Aug-99	5.8	3.5	0.3	16.2	2.8
22-Aug-99	5.4	3.6	0.5	8.4	3.6
13-Sep-99	1.9	3.3	0.3	9.9	3.2
26-Oct-99	1.2	3.1	0.5	1.6	3.5
16-Nov-99	10.7	3.2	0.5	12.0	3.0

ZOOPLANKTON AVERAGE STANDING STOCK

The 1999 GCL zooplankton community included 3 copepods (*Epischura nevadensis*, *Skistodiaptomus oregonensis*, *Diacyclops thomasi*), and 6 cladocerans (*Daphnia longiremis*, *Daphnia pulex*, *Bosmina longispina*, *Bosmina longirostris*, *Holopedium gibberum* and *Polyphemus pediculus*). Rotifers were not included in our counts. These species designations agree with LeBrasseur and Kennedy (1972) except that they identified all of their bosminids as *Bosmina coregoni*. Since 1973, taxonomic designations for *D. thomasi* and *S. oregonensis* have changed and we have used these more recent names.

In Table 4, data for the two bosminids have been combined because *B. longirostris* comprised > 95% of their joint biomass. Similarly, data for the two daphnids have been combined because *D. longiremis* comprised > 95% of daphnid joint biomass. Copepodid and adult *D. thomasi* and *S. oregonensis* were counted separately, but have been combined in Table 4. *Holopedium gibberum* and *Polyphemus pediculus* were also counted separately, but only *H. gibberum* was abundant enough to be included in Table 4.

The dominant species groups (Table 4) both by numbers and biomass in GCL were bosminids and *D. thomasi*. This is reflected in average eggs per L. The largest bodied species were *E. nevadensis*, *D. pulex*, *H. gibberum* and *P. pediculus*.

Table 4. Mean GCL1999 (June-November) zooplankton density, biomass, mean weights and egg densities.

Attribute	*Daphnia*	*H. gibberum*	*Bosmina*	*S. oregonensis* cop & adults	*S.oregonensis* nauplii	*D. thomasi* cop & adults	*D.thomasi* nauplii	*E. nevadensis*
Mean density (per L)	0.02	0.58	3.93	0.13	0.45	2.04	0.43	0.01
Mean weight per individual (µg dw)	2.03	2.53	1.75	3.91	0.23	1.66	0.18	14.45
Mean biomass (µg L^{-1} dw)	0.04	1.56	8.41	0.49	0.10	3.19	0.07	0.09
Eggs per L	0.00	0.09	0.76	0.00		0.14		
Mean eggs per individual	0.17	0.28	0.33	0.13		0.18		

ZOOPLANKTON SEASONALTRENDS

During 1999, GCL zooplankton density (Figure 5) and biomass (Figure 6) were dominated by Bosmina, *D. thomasi,* and *H. gibberum.* Maximum density and biomass were observed during September and October, however, GCL zooplankton exhibit substantial year to year variability (LeBrasseur and Kennedy 1972). Shortreed and Morton (unpublished), analyzed data collected in 1992, 1993, 1994, 1995 (4 zooplankton samples collected May-August) and 1998 (11 zooplankton samples collected May-September). In two of the 5 years, there was only one *Bosmina* peak in late summer as in 1999. In an additional two of the five years, maximum *Bosmina* biomasses were measured in the late summer, but biomasses were relatively low throughout. In one of five years (1983), maximum *Bosmina* biomass was observed in June. Similar results were obtained for *Daphnia*. Data for *Daphnia* were available for seven years (the 5 above plus 1983 and 1984). One year showed a strong fall peak in *Daphnia* biomass. Five had low *Daphnia* biomasses and the single spring peak was

observed in 1984 (different year from *Bosmina* above). Data for *D. thomasi* were available for five years and all showed highest biomasses in the spring in accord with our observations of this species in 1999. Data for *S. oregonensis* were available for five years and biomasses were very low in all but one year. In summary, almost any seasonal pattern seems to be possible and the 1999 pattern is not exceptional.

During 1999, total zooplankton biomass averaged through June-October was 13.95 µg L^{-1} dry weight (based on eight sample dates each based on 4 samples taken at night over 25 m using 100 µm mesh). LeBrasseur and Kennedy (1972) reported average May-October wet weights of 0.5 g m^{-2} during an unfertilized year (1969) and 5.3 g m^{-2} wet weight during a fertilized year (1970). They used a 100 µm mesh net hauled over 50 m. Assuming dry weight to be about 14% of wet weight, their summer averages translate to 1.4 µg L^{-1} dry weight during the unfertilized year and 14.84 µg L^{-1} dry weight during the fertilized year. Our treated year zooplankton biomass observation for 1999 is quite close to the treated year value observed by LeBrasseur and Kennedy (1972) for their treated (1970) to untreated (1969) year comparison. Shortreed et al. (2001), listed average GCL biomass as 435 mg m^{-2} dry weight. The data were described as having been derived from multiple years of monthly sampling. Assuming a 50 m haul depth, the Shortreed et al. (2001) biomass average equals 8.7 µg L^{-1} dry weight that is somewhat lower than our estimate and the estimates published by LeBrasseur and Kennedy (1972). From this, we conclude that 1999 was within the expected range for zooplankton biomass observed during treated years at GCL.

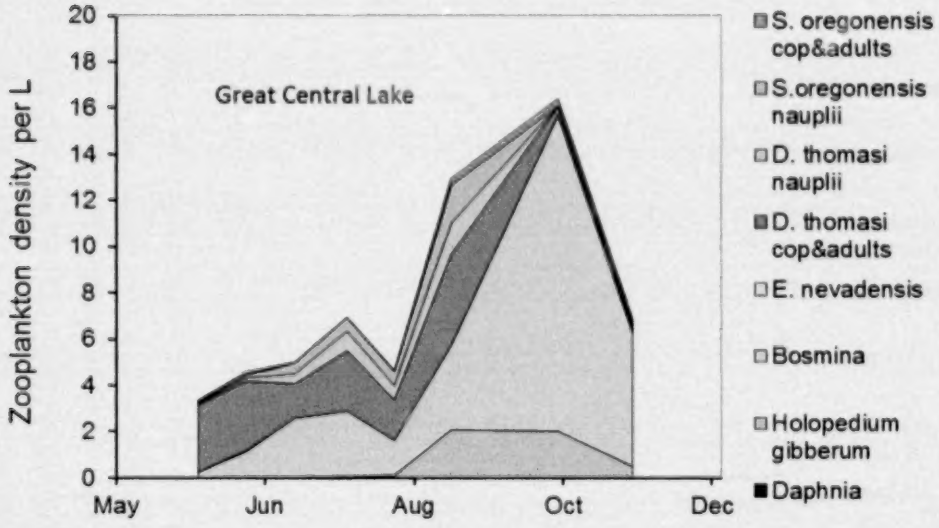

Figure 5. 1999 GCL zooplankton density per L. Details are available in Appendix 1.

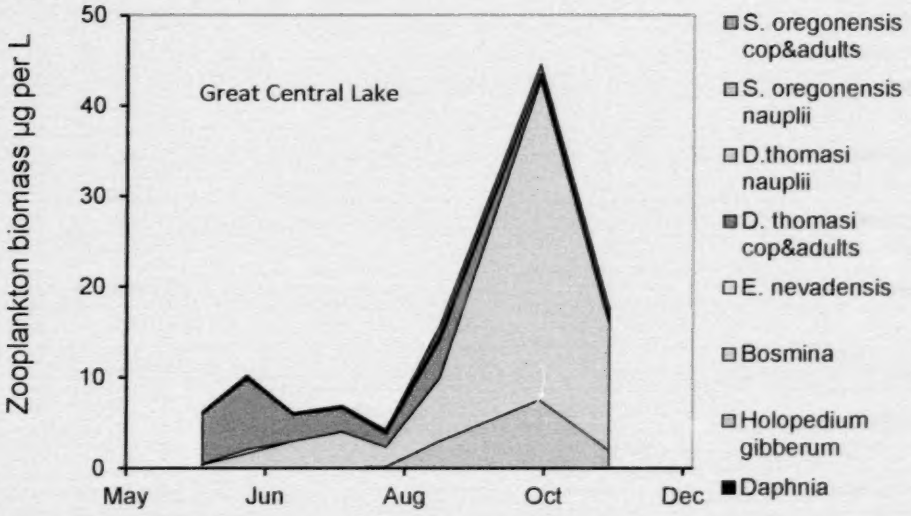

Figure 6.1999 GCL zooplankton biomass µg L^{-1} dry weight. Details are available in Appendix 1.

ZOOPLANKTON PRODUCTION

Mean summer rates of production for the three species accounting for >95% of the GCL zooplankton biomass consumed by fish, are summarized in Table 5. Compared to other lakes, even when fertilized, GCL zooplankton production during 1999 appears relatively low. For example, GCL production rates were lower than recorded at Woss Lake (Hyatt et al. 2011) during 2005 (Woss Lake *Daphnia* = 0.073, *Bosmina* = 0.329, *D. thomasi* = 0.592 µg L^{-1} d^{-1} dw) and Vernon Lake 2005 (Vernon Lake *Daphnia* = 0.59, *Bosmina* = 0.36, *D. thomasi* = 0.16 µg L^{-1} d^{-1} dw). This was a bit surprising, especially the values for *D. thomasi*, given that average TP in GCL was 3.5 µg L^{-1} compared to average 2005 TP concentrations in Woss Lake (4.3 µg L^{-1}) and Vernon Lake (4.1 µg L^{-1}). However, spring-summer of 1999 was the coolest year for the Somass watershed in more than a decade (Hyatt et al. 2015) so perhaps this accounts for the relatively low production values observed that year. By contrast, it was not surprising that GCL production rates were much lower than in Skaha Lake where 2005-08 TP averaged 7.4 µg L^{-1} and daily production for *Daphnia*, *Bosmina*, and *D. thomasi* averaged 0.58, 0.12, and 0.67 µg L^{-1} d^{-1} dw respectively (McQueen et al. 2014).

Table 5. Average (3 June – 25 November) zooplankton standing stock, egg density, and production in Great Central Lake 1999.

Species	Summer average biomass $\mu g\ L^{-1}$ (dw)	Average egg density L^{-1}	Summer average production $\mu g\ L^{-1}\ d^{-1}$ (dw)	P/B per day	Summed P/B
Daphnia	0.039	0.003	0.001	0.024	4.2
Bosmina	8.408	0.756	0.219	0.026	4.6
D.b. thomasi	3.193	0.135	0.041	0.013	2.2

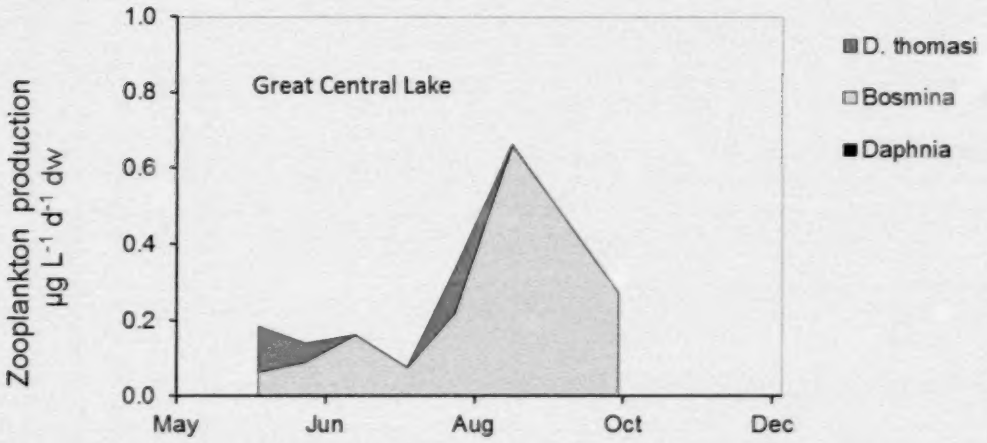

Figure 7. Average zooplankton production in Great Central Lake 1999.

The 1999 seasonal pattern of zooplankton production for GCL followed trends in biomass (i.e. low production during the spring and increased production during the fall (Figure 7). This pattern did not reflect annual trends in either TP or chlorophyll a, both of which remained constant through the season (Table 3). Perhaps this was due to the weekly pattern of fertilization that tends to promote increased production by all phytoplankton and accumulation of larger less-grazable algal cells.

SOCKEYE SALMON DENSITY, LENGTHS, AND WEIGHTS

Juvenile sockeye made up 100% of trawl-caught fish and 1999 juvenile sockeye salmon densities were about average for GCL (Table 6). For comparison fall GCL densities based on the 10 year preceding 1999, averaged 1883 ha^{-1} (maximum = 3800 ha^{-1}, minimum = 780 ha^{-1}, (Hyatt and Rankin, unpublished observations). Based on mean

lengths (Table 7), it appears that growth stopped from mid to late summer and then resumed in the fall (Figure 8). Compared to average weights from the previous 10 years (Shortreed et al. 2001), juvenile sockeye grew very slowly during 1999 (10 year GCL fall juvenile sockeye mean weight 3.7 g (min = 2.3 g, max = 6.6 g). The different seasonal patterns of juvenile sockeye salmon growth observed in Sproat Lake and GCL (Figure 8) reflect observations of between lake differences in patterns of zooplankton biomass and production. In GCL, both were higher in the fall and in Sproat Lake both were higher in the spring suggesting that sockeye seasonal growth potential is tightly coupled to changes in zooplankton abundance.

Table 6. GCL acoustic-and-trawl based estimates of juvenile sockeye abundance.

Survey Date	Pop. Est.(Total)	95% Con. Int.	Density per ha	95% CI per ha
21-Jun-99	16,518,118	4,755,972	3,239	933
21-Jul-99	10,082,107	4,898,991	1,977	961
29-Nov-99	7,430,561	2,885,262	1,457	566

Table 7. GCL 1999 trawl-based juvenile sockeye lengths and weights.

Survey Date	n	Mean length (mm)	Mean weight (g)	Stdev. length	Stdev. weight	95% CI length	95% CI weight
21-Jun-99	270	29.77	0.21	3.61	0.18	0.43	0.06
2-Aug-99	205	42.42	0.73	10.04	0.60	1.37	0.18
16-Sep-99	200	41.90	0.75	7.99	0.60	1.11	0.18
29-Nov-99	196	58.49	1.88	5.25	0.60	0.73	0.15

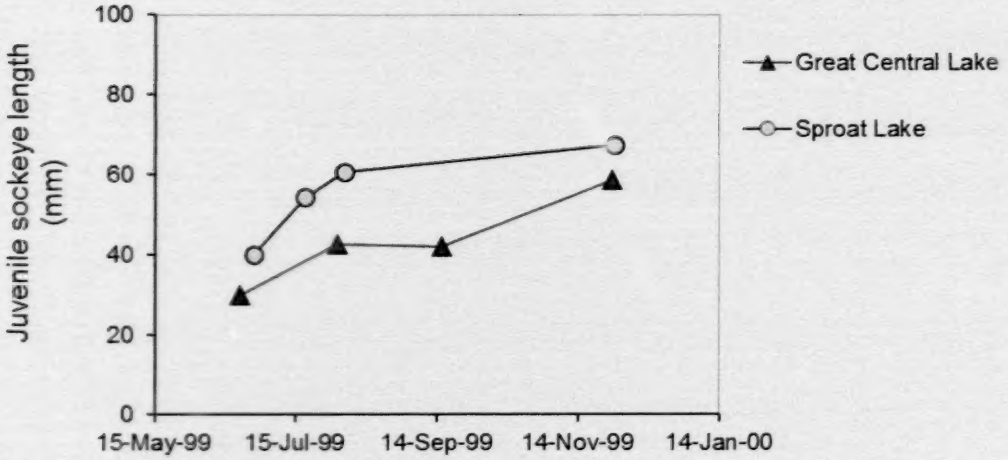

Figure 8. Juvenile sockeye lengths with respect to time of year for GCL and Sproat Lake.

JUVENILE SOCKEYE DIETS

During the summer-fall of 1999, stomachs from 159 juvenile sockeye were examined (Table 8). The most important prey included *Bosmina*, *D. thomasi* adults & copepodids, and adult insects (dipterans). Mean weights based on field data (Table 9) were used to convert crustacean zooplankton densities per fish stomach (Table 8) to weights per stomach (required for use in the bioenergetics model). In the case of chironomids and adult dipterans, mean weight ranges came from Robinson and Barraclough (1972). Both upper and lower estimates have been used to estimate two versions of "proportion of each prey type consumed by juvenile sockeye" (Table 8).

Table 8. Stomach contents of juvenile sockeye captured in GCL on five dates through the summer-fall of 1999.

Sampling Date	n	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	*S. oregonensis* adult & cop	*S. Oregonensis* nauplii	*Epischura*	*D. thomasi* adult & cop	*D. thomasi* nauplii	Adult dipterans	Chironomid larvae	Total
Consumption per fish (number of prey per fish stomach)													
22-Jun-99	33	0.0	0.0	0.0	18.2	0.0	0.0	0.0	24.1	0.0	0.0	0.0	
21-Jul-99	34	0.1	0.0	0.0	147.1	0.0	0.0	0.4	23.1	0.0	0.6	0.0	
09-Aug-99	33	0.2	0.1	0.0	161.2	0.0	0.0	0.1	6.6	0.0	4.5	0.0	
19-Sep-99	30	1.5	22.1	0.4	238.4	0.0	0.0	0.3	6.1	0.0	1.7	0.0	
29-Nov-99	29	0.2	0.6	0.0	478.2	0.0	0.0	2.1	8.5	0.0	0.0	0.0	
Weights consumed µg dw (using lower estimates for insects and chironomids)													
22-Jun-99		0	0	0	36	0	0	0	48	0	0	0	84
21-Jul-99		0	0	0	294	0	0	8	46	0	32	0	382
09-Aug-99		1	0	0	322	0	0	1	13	0	227	0	565
19-Sep-99		7	88	2	477	0	0	7	12	0	87	0	680
29-Nov-99		1	2	0	956	0	0	43	17	0	0	0	1019
Weights consumed µg dw (using higher estimates for insects and chironomids)													
22-Jun-99		0	0	0	36	0	0	0	48	0	0	0	84
21-Jul-99		0	0	0	294	0	0	8	46	0	226	6	581
09-Aug-99		1	0	0	322	0	0	1	13	0	1591	0	1929
19-Sep-99		7	88	2	477	0	0	7	12	0	607	0	1200
29-Nov-99		1	2	0	956	0	0	43	17	0	0	0	1019
Proportion of each prey type consumed using lower weight estimates													
22-Jun-99		0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.57	0.00	0.00	0.00	1
21-Jul-99		0.00	0.00	0.00	0.77	0.00	0.00	0.02	0.12	0.00	0.08	0.00	1
09-Aug-99		0.00	0.00	0.00	0.57	0.00	0.00	0.00	0.02	0.00	0.40	0.00	1
19-Sep-99		0.01	0.13	0.00	0.70	0.00	0.00	0.01	0.02	0.00	0.13	0.00	1
29-Nov-99		0.00	0.00	0.00	0.94	0.00	0.00	0.04	0.02	0.00	0.00	0.00	1
Proportion of each type of prey consumed using upper insect weight estimates													
22-Jun-99		0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.57	0.00	0.00	0.00	1
21-Jul-99		0.00	0.00	0.00	0.51	0.00	0.00	0.01	0.08	0.00	0.39	0.01	1
09-Aug-99		0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.01	0.00	0.82	0.00	1
19-Sep-99		0.01	0.07	0.00	0.40	0.00	0.00	0.01	0.01	0.00	0.51	0.00	1
29-Nov-99		0.00	0.00	0.00	0.94	0.00	0.00	0.04	0.02	0.00	0.00	0.00	1

Table 9. Mean weights (µg dry weight) for crustacean zooplankton, chironomids, and dipterans.

Daphnia	*Holopedium*	*Polyphemus*	*Bosmina*	*S. oregonensis*	*Epischura*	*D. thomasi*	Adult dipterans	Chironomid larvae
5	4	5	2	4	20	2	50-350	11-196

NOCTURNAL DEPTH DISTRIBUTION OF JUVENILE SOCKEYE SALMON

In GCL, on three dates during 1999, field crews conducted acoustic surveys of the same transect (transect 6) approximately every half hour from just before sunset to just after sunrise. The numbers in the Table 10 represent % of the total number of fish recorded during the sampling session (sundown to sunrise). From these tables, it becomes immediately apparent that as the sun set, fish began to appear from an area or depth of the lake outside the sampling transect. The majority then aggregated between 5-30 m (shaded area) where they fed. Then near sun-rise, they began to disappear from the sampling transect. During November, when the lake was relatively isothermal, the fish were found slightly deeper, but still aggregated between 5-40 m water depth.

One issue with these data is that the echosounder was unable to detect fish between 0-2 m, and due to the small cross-sectional area included in the beam at shallow depths, acoustics results may be less accurate for targets between 2-5 m. This means that the fish could have been present in 0-5 m water, but would have been under-represented in the echograms summarized in Table 10. We do know from the diet information (Table 9) that they had dipteran adults in their stomachs and therefore, must have at times, fed at or near the lake surface. However, the weight of evidence based on surface trawling and direct observations during years of surveys of Great Central and many other coastal lakes indicates that juvenile sockeye seldom occupy surface waters in any numbers or for long unless light levels there are low (i.e. a half to full-moon will suppress surface occupation) and temperatures are favourable (i.e. < 17 ^{o}C).

Interpretation of the diel data is quite important because it influences the residence temperatures used in the bioenergetics model. During August (Table 10), >85% of the fish appeared to be aggregated between 5-30 m depth, and in September >70% were aggregated closer to the surface between 0-15m depth. Given that the GCL fish consumed substantial quantities of adult chironomids, we have to assume that they spent some of their time at the surface where they may not have been detected by the echosounder. We have therefore assumed that during the stratified period (June – October), juvenile sockeye experienced daily temperatures averaged over 0-15 m.

Table 10. Nocturnal depth distribution (% of total) of juvenile sockeye salmon in GCL recorded on 09 August, 16 September, and 30 November. The shaded areas represent "concentration depths", defined as the depth distribution that includes >85% of the fish sampled during the time interval. Mean water temperatures are shown in blue numbers (°C).

09-Aug-99		Depth (m)									
Time In	Time Out	0-5	5-10	10-15	15-20	20-30	30-40	40-50	50-60	60-70	70-80
20:23	20:42										
20:45	21:04	0	0	0	0	1	0	0	0	0	
21:15	21:30	0	1	2	1	0	0	0	0	0	
21:40	21:54	1	4	3	1	0	0	0	0	0	
22:55	23:08	0	3	3	3	1	0	0	0	0	
0:47	1:02	0	4	4	3	1	0	0	0	0	
2:00	2:14	1	3	4	3	1	0	0	0	0	
3:10	3:27	0	2	5	3	1	0	0	0	0	
4:10	4:25	1	3	5	3	1	0	0	0	0	
5:00	5:16	0	3	3	3	2	0	0	0	0	
5:42	5:56	0	1	1	1	4	1	0	0	0	
6:10	6:26	0	1	0	0	1	1	0	0	0	
Mean temperature		21	12	11	8	6	5	5	5	5	

16-Sep-99		Depth (m)									
Time In	Time Out	0-5	5-10	10-15	15-20	20-30	30-40	40-50	50-60	60-70	70-80
19:20	19:36	0	0	1	1	0	0	0	0		
19:50	20:05	0	3	1	0	0	0	0	0		
22:05	22:19	0	8	4	4	1	0	0	0		
0:05	0:21	0	6	5	4	1	0	0	0		
2:06	2:22	0	7	4	2	0	0	0	0		
3:31	3:48	0	7	5	1	0	0	0	0		
5:02	5:18	1	7	4	1	0	0	0	0		
5:35	5:51	1	4	2	1	1	0	0	0		
5:55	6:10	0	2	2	1	1	0	0	0		
6:30	6:45	0	0	1	1	1	1	0	0		
Mean temperature		19	16	10	7	6	5	5	5		

30-Nov-99		Depth (m)

Time In	Time Out	0-5	5-10	10-15	15-20	20-30	30-40	40-50	50-60	60-70	70-80
16:22	16:39	0	0	0	0	0	0	0	0	0	0
16:42	16:55	0	0	0	0	0	0	0	0	0	0
16:53	17:11	0	0	0	0	1	0	0	0	0	0
17:13	17:26	0	1	1	1	1	0	0	0	0	0
17:28	17:42	0	1	2	1	1	0	0	0	0	0
17:52	18:06	0	1	2	2	1	0	0	0	0	0
19:30	19:43	0	1	1	1	2	0	0	0	0	0
19:55	20:10	0	1	2	2	2	0	0	0	0	0
20:32	20:47	0	1	1	1	2	0	0	0	0	0
20:56	21:12	0	1	2	2	2	0	0	0	0	0
22:45	23:02	0	1	2	2	2	1	0	0	0	0
23:05	23:24	0	1	2	2	2	1	0	0	0	0
1:11	1:30	0	1	1	1	2	1	0	0	0	0
3:47	4:05	0	1	1	2	2	1	0	0	0	0
5:15	5:31	0	1	1	1	2	0	0	0	0	0
5:50	6:09	0	1	1	1	2	0	0	0	0	0
6:34	6:51	0	1	1	1	2	0	0	0	0	0
7:10	7:28	0	1	1	2	2	0	0	0	0	0
7:40	7:59	0	0	0	0	1	0	0	0	0	0
7:59	8:18	0	0	0	0	0	0	0	0	0	0
Mean temperature		7	7	7	7	7	5	5	5	5	5

JUVENILE SOCKEYE BIOENERGETICS AND FOOD CONSUMPTION

Simulations were run for the period when fish weights were available (i.e. 21 June – 28 November) and separate simulations were based on each of the two diet data sets described above (Table 10). Water temperatures were averaged from recorded temperatures between 0-15 m depth. This decision resulted in mid-summer residence temperatures that were higher than they would be if temperatures were averaged over a greater depth interval. However, sensitivity analysis showed that even when daily residence temperatures were averaged over a much greater depth (i.e. 11 $^{\circ}$C based on 0-40m depth) daily consumption was reduced by only 5%. Mean weights of fish at the start and end of the simulations were based on field data (Table 7, Figure 7). Model weights-at-age were compared with weights observed in the field and in order to achieve a good fit between field and simulated mean fish weights-at-age, model parameters CB = (slope of allometric mass function), CTO = (water temperature corresponding to 0.98 of the maximum consumption rate), and CTM = (the water temperature (>CTO) at which dependence is still 0.98 of the maximum rate) in the

model 3 consumption equation (see details in Hanson et al. 1997, e.g. Figure 3) were adjusted to -0.6, 13 and 13 respectively, (Figure 9).

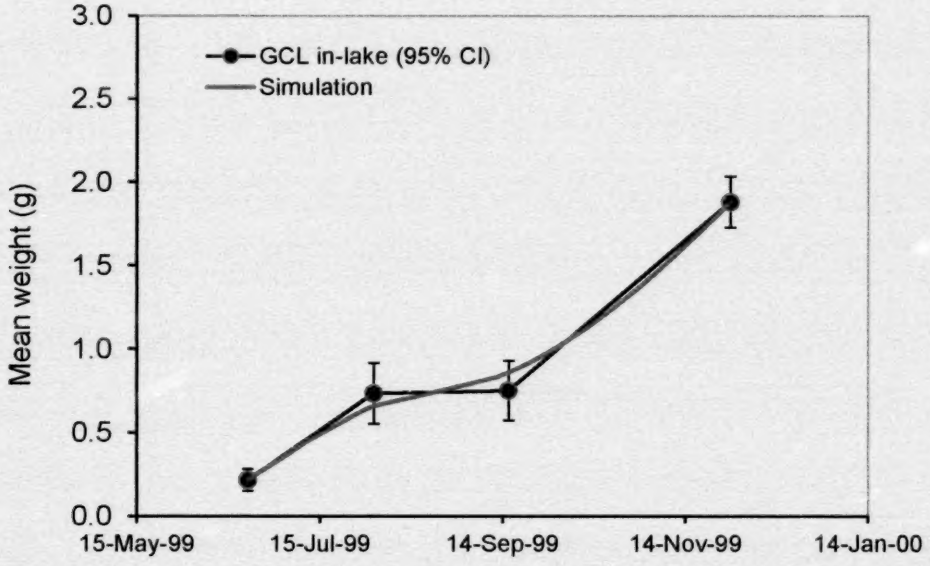

Figure 9. Field measured average weights (± 95% CI) of juvenile sockeye salmon and average weights simulated using the bioenergetics model.

The bioenergetics model calculates food consumption based on mean body weights observed in the field (0.2 g on 21 June at the beginning of the simulation and 1.8 g on 29 November at the end of the simulation period (162 days)). Model inputs also include daily water temperatures occupied by the fish and changing proportions (by weight) of each food type found in the guts of average fish (from Table 8). Through an iterative process, the model estimates the amount of food the fish would have to have eaten in order to grow as fast as it did grow in the field. Therefore, if water temperatures are reasonably accurate, and simulated and measured weights-at-age are in close agreement, then calculated rates of food consumption are likely to be accurate.

From Figure 9, we see that field and simulated weights-at-age were in good agreement and therefore, we assume that simulated rates of food consumption (Figures 10 and 11) represent reasonably accurate approximations of actual food consumption in the field.

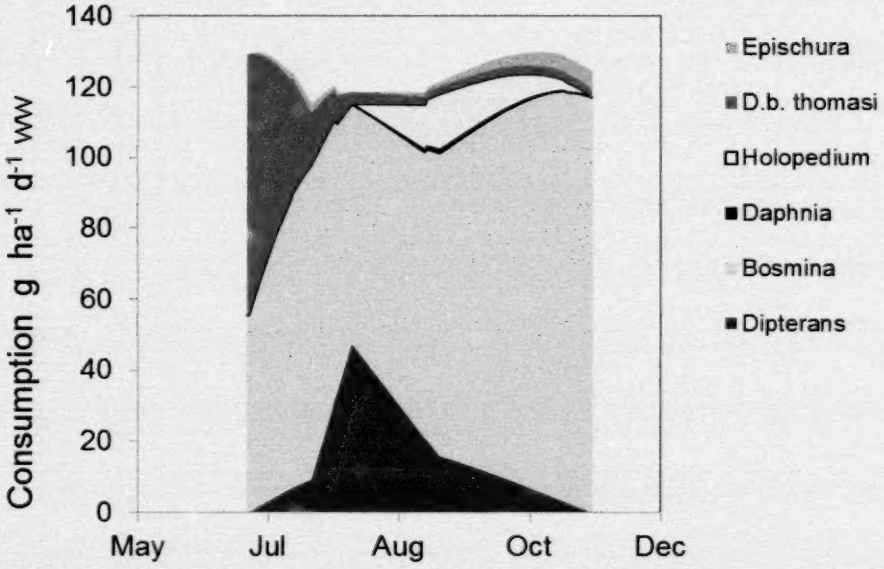

Figure 10. Simulation 1 (minimum weights for dipterans): Bioenergetics-based estimates of GCL food consumption by juvenile sockeye salmon (g per ha wet weight per day) assuming that the fish feed in the top 30 m of lake water.

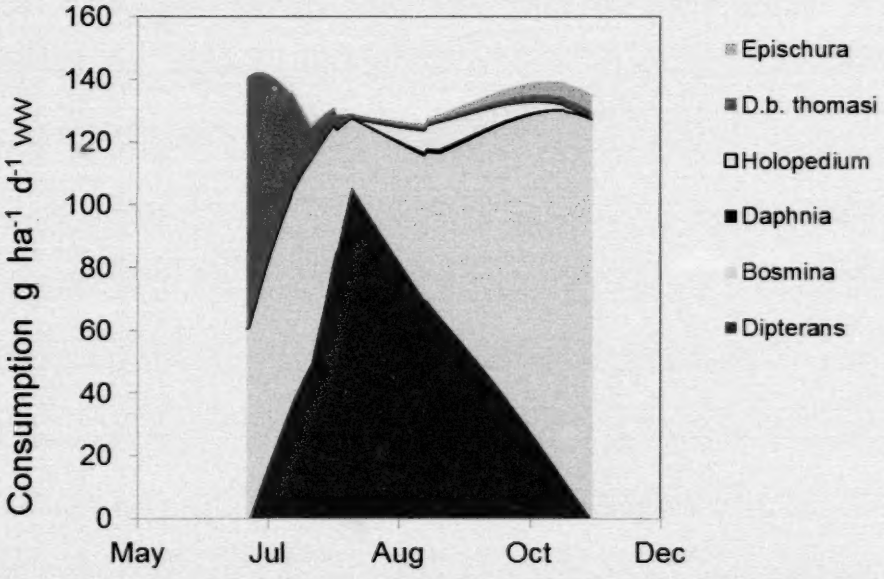

Figure 11. Simulation 2 (maximum weights for dipterans): Bioenergetics-based estimates of GCL food consumption by juvenile sockeye salmon (g per ha wet weight per day) assuming that the fish feed in the top 30 m of lake water.

In simulation 1 (Figure 10) dipterans were assumed to be in the smaller weight class reported by Robinson and Barraclough (1972) and in simulation 2, dipterans were assumed to be in the larger weight class reported by Robinson and Barraclough (1972). The true field value probably lies somewhere between the two. The most important zooplankton preys were cyclopoids (*D. thomasi*) early in the season and *Bosmina* later in the season. Because the units (g ha^{-1} d^{-1}) are not intuitive, the following assumptions and conversions may be helpful.

Part 1: LeBrasseur and Kennedy (1972) found the following night time depth distributions for zooplankton. *Bosmina* and *Holopedium* 0-10 m, *Daphnia* 20-30 m, D. *thomasi* 20-40 m. During 1999, most fish were observed at 0-30 m (Table 11). We sampled zooplankton from 0-25 m. We calculated average consumption over 0-30 m.

Part 2: During 1999, mean zooplankton biomass was approximately 15 µg L^{-1} dry weight. Mean consumption by fish was 120 g ha^{-1} d^{-1} wet weight. To convert from g ha^{-1} wet weight to µg L^{-1} dry weight, we divide by 2100. To convert from µg L^{-1} dry weight to g ha^{-1} wet weight we multiply by 2100. The basis for these conversions is as follows (1) 15 µg L^{-1} dry weight = 15 mg m^{-3} dw, (2) 15 mg m^{-3} dw = (7*15) = 105 mg m^{-3} wet weight [7 = wet-dry conversion], (3) 105 mg m^{-3} wet weight = (30*105) = 3150 mg m^{-2} wet weight [30 = water depth in m], (4) 3150 mg m^{-2} wet weight = (3150/1000) = 3.15 g m^{-2} wet weight, (5) 3.15 g m^{-2} wet weight = (10000*3.15) = 31500 g ha^{-1} wet weight. Therefore (1) to convert from g ha^{-1} wet weight to µg L^{-1} dry weight, we divide by (31500/15) = 2100, (2) to convert from µg L^{-1} dry weight to g ha^{-1} wet weight we multiply by (15/31500) = 2100.

Part 3: During 1999, the average density of sockeye per ha was 1851 ha^{-1}. (1) Average density m^{-2} was (1851/10000) = 0.1852 m^{-2}. (2) Average density m^{-3} was (0.1852/30) = 0.00617 m^{-3}. Therefore (3) the average water volume occupied by one juvenile sockeye was (1/0.00617) = 162 m^3.

Part 4: During 1999, the average *Bosmina* density per L was 3.935 L^{-1}. Therefore the average *Bosmina* density per cubic meter was 3935 m^3.

Now we can use these assumptions and conversions to estimate the average impact that juvenile sockeye may have had on their prey. Simulation 1 (minimum dipteran weights), predicted that on average through 1999, juvenile sockeye consumed 88 g ha^{-1} d^{-1} wet weight of *Bosmina* (Figure 10). The average standing stock biomass of *Bosmina* was 8.5 µg L^{-1} dry weight (Figure 6) which converts to (2100*8.5) = 18,017 g ha^{-1} wet weight *Bosmina*. Therefore, fish consumption averaged about 0.5% per day of the *Bosmina* standing stock.

Looking at this from the perspective of density, we know that average consumption by sockeye was 88 g ha^{-1} ww *Bosmina* per day. Therefore one fish consumed (88/1851) = 0.0475 g ww *Bosmina* per day. This is 47,542 µg ww d^{-1}, which is 6792 µg dw d^{-1}. The average weight for one *Bosmina* 2 µg dw. From this we conclude that one fish consumed an average of 3396 *Bosmina* per day. Since average *Bosmina* density per L

was 3,935 L^{-1}, each day one fish had to capture all of the *Bosmina* in 863 L of water. Since each fish occupied an average of 162 m^3 = 162,000 L of water, it must have consumed (863/162,000) = 0.5% of the *Bosmina* population per day. This is the same result obtained above using weights.

Extending this analysis to other zooplankton, we have the results summarized in Table 11.

Table 11. Average 1999 GCL rates of consumption by juvenile sockeye salmon.

	Daphnia	*Holopedium gibberum*	*Bosmina*	*S. oregonensis* cop&adults	*D. thomasi* cop&adults	*E. nevadensis*	Adult dipterans	Chironomid larvae
Mean biomass (µg L^{-1} dw)	0.0	1.6	8.4	0.5	3.2	0.1	nd	nd
Mean biomass g m^2 ww	0.0	0.3	1.8	0.1	0.7	0.0	nd	nd
Mean biomass g ha^{-1}	81	3342	18017	1042	6841	187	nd	nd
Mean production g ha^{-1} d^{-1}	2.0	nd	468	nd	87	nd	nd	nd
Consumption simulation-1 g ha^{-1} d^{-1}	1.0	5.6	88.5	0.0	11.6	1.9	15.8	0.0
% standing consumed d^{-1}	1.2	0.2	0.5	0.0	0.2	1.0	nd	nd
% production consumed d^{-1}	50.6		18.9		13.2			
Consumption simulation-2 g ha^{-1} d^{-1}	1.0	3.2	67.1	0.0	10.8	1.9	50.0	0.2
% standing consumed d-1	1.2	0.1	0.4	0.0	0.2	1.0	nd	nd
% production consumed d-1	50.6		14.3		12.3			

Table 11 suggests that there is little likelihood that juvenile sockeye salmon could have had much influence on zooplankton standing stocks. In all cases, zooplankton replacement rate (i.e. production) was always greater than losses due to fish consumption. However, when we compare daily rates of consumption by fish (Figures 10 and 11) with zooplankton densities (Figure 5) and biomass (Figure 6), we see that during the spring, zooplankton biomasses were low, but rates of consumption were as high as they were at any other time of year (Table 12). This suggests that during the spring, the fish may have suppressed the developing zooplankton populations.

Comparisons of daily rates of consumption with zooplankton standing stocks and daily rates of production (Table 12) suggest that juvenile sockeye could have relatively strong top-down impacts on *Bosmina* during the spring, *Daphnia* during the summer and *D. thomasi* during the fall. None of the rates suggest that fish could have caused declines in any of the populations, but given that the estimates do not account for other sources of zooplankton mortality we must conclude that during 1999 there was a relatively close

balance between zooplankton production and consumption by fish. This was especially the case for *Daphnia*. Because spring *Daphnia* densities were very low, very few appeared in fish stomachs and therefore average daily consumption during the spring was uncertain. Given this uncertainty, it is conceivable that the very low *Daphnia* population densities may have been due to consumption by fish.

Table 12. Percent of zooplankton standing stock and production consumed per day by juvenile sockeye.

	Daphnia		*Bosmina*		*D. thomasi*	
Sampling Date	% standing stock	% production	% standing stock	% production	% standing stock	% production
3-Jun-99	0		6		1	
22-Jun-99	0	0	2	42	0	29
12-Jul-99	0	0	1	45	1	32
2-Aug-99	0	0	1	23	0	
21-Aug-99	0	21	2	46	0	
13-Sep-99	2	73	1	18	0	1
26-Oct-99	0	22	0	8	0	81
25-Nov-99	0	5	0	21	0	

Finally using *Bosmina* as an example, we can estimate the volume of water that a fish would need to clear of prey in order to satisfy its' daily food requirements. *Bosmina* density averaged 3.935 L^{-1} (approximately 4 L^{-1}), and each juvenile sockeye consumed an average of 3396 *Bosmina* per day. If we assume that a juvenile sockeye could detect all *Bosmina* within a hemisphere having a radius of 5 cm, (i.e. could see *Bosmina* up to 5 cm distant from the eye), then a fish would need to swim only 12.8 cm (cylinder 10 cm diameter and 12.8 cm long = ($12.8^* \pi 5^2$) = 1000 cm^3 = 1 L) in order to encounter and capture 4 *Bosmina*. Therefore, a fish would need to swim a distance of 10,862 cm (108 m) to capture enough *Bosmina* to satisfy daily requirements. Assuming a mean fish length of 3 cm and an average swimming speed of 2 body lengths per second (relatively slow swimming speed), only 30 minutes of swim time plus handling time would be required to capture 3396 *Bosmina*. Also, since each fish occupied an average volume of 162 m^3, competition would have been minimal.

We conclude by noting that during 1999, GCL was fertilized and Robinson and Barraclough (1972) showed that fertilization increased zooplankton standing stocks by about a factor of 10. Had the lake not been fertilized, there is little doubt that an average density of 1851 fish ha^{-1} would have seriously depressed zooplankton standing stocks, with an inevitable density-dependent effect on fish growth rates.

RESULTS AND DISCUSSION SPROAT LAKE

Table 13. Sproat Lake oxygen and temperature profiles. The dark area represents temperatures >17^{O}C which are usually avoided by juvenile sockeye salmon.

	Temperature (°C)				Oxygen (mg / L)			
Depth	27-Jun-99	19-Jul-99	05-Aug-99	30-Nov-99	08-Jun-99	27-Jun-99	05-Aug-99	30-Nov-99
0	14.7	21.5	22.2	7.3	14.5	10.1	8.0	10.4
1	14.7	20.8	22.1	7.4	14.6	10.1	8.1	10.3
2	14.5	19.5	21.7	7.4	14.6	10.1	8.1	10.2
3	14.5	19.2	21.3	7.4	14.5	10.1	8.2	10.2
4	14.4	18.6	21.0	7.4	14.5	10.1	8.2	10.2
5	14.3	17.0	21.1	7.4	14.3	10.1	8.3	10.2
6	13.7	14.9	20.6	7.4	13.9	10.2	8.6	10.2
7	13.7	14.0	20.2		13.4	10.2	8.8	
8	13.3	11.6	17.4	7.4	12.7	10.2	9.5	10.1
9	12.6	10.5	14.6	7.4	11.7	10.3	9.9	10.1
10	11.6	9.4	13.1	7.4	11.0	10.6	10.5	10.1
11	11.2	8.6	12.4		10.2	10.6	10.3	
12	10.4	8.3	12.9	7.4	9.3	10.8	10.5	10.1
13	9.5	7.6	12.2	7.4	8.8	10.9	10.6	10.1
14	9.0	7.4	10.3	7.4	8.3	10.9	10.7	10.1
15	8.5	7.3	9.6		7.7	10.9	10.7	
16	8.3	7.2	8.8	7.4	7.3	10.8	10.7	10.1
17	8.2	7.0	8.7	7.4	7.1	10.8	10.6	10.0
18	8.2	6.8	8.2	7.4	6.9	10.7	10.6	10.0
19	7.5	6.5	8.0	7.4	6.8	10.6	10.5	10.0
20	7.4	6.3	7.8		6.6	10.7	10.5	
21	7.0	6.0	7.7	7.3	6.5	10.6	10.5	9.9
22	6.8	5.8	7.5	7.1	6.3	10.5	10.2	9.9
23	6.6	5.5	7.4	7.0	6.3	10.3	10.2	9.9
24	6.5	5.5	7.3		6.1	10.4	10.2	
25	6.4	5.4	7.4	6.9	6.0	10.3	10.3	10.0
26	6.3	5.4			5.9	10.3		
27	6.3	5.3	7.2	6.9	5.8	10.2	10.0	10.0
28	6.3	5.4			5.8	10.6		
29	6.1	5.2	7.4	6.8	5.7	10.0	10.2	10.0
30	6.0	5.3				10.4		

TEMPERATURE AND OXYGEN

The Sproat Lake thermocline formed at 10-13 m in early summer. Surface water warmer than 17°C extended from the surface down to approximately 8 m depth. Temperatures warmer than 17°C are associated with negative growth (Brett et al. 1969) and are avoided by juvenile sockeye salmon (Levy 1990, 1991) (Table 13).

WATER CHEMISTRY

Sproat Lake macro-nutrient concentrations were very low confirming its oligotrophic status. Nitrate concentrations declined rapidly through the season and then increased at turnover in association with increased algal senescence. Total phosphorus (TP) concentrations remained constant. Chlorophyll a concentrations remained stable through the summer suggesting that algal cells may have been grazed as quickly as they were produced. The fall chlorophyll a increase may have been due to reduced fall grazing pressure by zooplankton (Table 14).

Table 14. Nitrate (NO_3), Total Phosphorus (TP) and corrected Chlorophyll a (Chl a = total chlorophyll minus phaeopigments) as µg per L.

	Epilimnion			Hypolimnion	
Date	NO_3	TP	Corrected Chl a	NO_3	TP
28-Jun-99	9.7	3.3	0.2	13.1	3.4
18-Jul-99	9.1	3.4	0.2	11.0	3.4
04-Aug-99	8.3	2.8	0.2	17.3	3.1
30-Aug-99	2.5	3.8	0.2	6.5	3.7
20-Sep-99	3.0	3.1	0.2	7.0	3.7
25-Oct-99	1.8	3.7	0.5	2.6	5.2
17-Nov-99	18.8	3.5	0.8	27.5	3.6

ZOOPLANKTON AVERAGE STANDING STOCK

The 1999 Sproat Lake zooplankton population comprised the same species observed at GCL. We found three copepods, (*Epischura nevadensis*, *Skistodiaptomus oregonensis*, *Diacyclops bicuspidatus thomasi*), and 6 cladocerans (*Daphnia longiremis*, *Daphnia pulex*, *Bosmina longispina*, *Bosmina longirostris*, *Holopedium gibberum* and *Polyphemus pediculus*). Rotifers were not included in our counts.

In Table 15, data for the two bosminids were combined because *B. longirostris* comprised > 95% of the joint biomass. Similarly, data for the two daphnids were combined because *D. longiremis* comprised > 95% of the joint biomass. Copepodid and adult *D. thomasi* and *S. oregonensis* were counted separately, but were combined in Table 15. *Holopedium gibberum* and *Polyphemus pediculus* were also counted separately, but only *H. gibberum* was abundant enough to be included in Table 15.

From Table 15, we see that the list of dominant zooplankton included not only *Bosmina* (almost all *B. longirostris*) and *D. thomasi* as in GCL, but also included *Daphnia* (almost all *D. longiremis*) and *Holopedium*. Densities and biomasses of the major groups were slightly higher in Sproat Lake (mean density = 9 L^{-1}, mean biomass = 18 µg L^{-1} dw) than in GCL (mean density = 8 L^{-1}, mean biomass = 14 µg L^{-1} dw). The differences are not greater because *S. oregonensis* were less abundant in Sproat than in GCL.

Table 15. Mean Sproat Lake 1999 (June-November) zooplankton density, biomass, mean weight, and egg numbers.

Attribute	*Daphnia*	*H. gibberum*	*Bosmina*	*S. oregonensis* cop&adults	*S. oregonensis* nauplii	*D. thomasi* cop&adults	*D. thomasi* nauplii	*E. nevadensis*
Mean density (per L)	1.13	1.01	4.11	0.08	0.21	1.63	0.71	0.05
Mean weight per individual (µg dw)	1.69	1.89	2.20	3.92	0.26	2.13	0.16	10.03
Mean biomass (µg L^{-1} dw)	2.03	1.81	9.00	0.28	0.05	4.16	0.10	0.54
Eggs per L	0.28	0.10	0.48	0.00		0.51		
Mean eggs per individual	0.21	0.22	0.12	0.31		0.49		

ZOOPLANKTON SEASONAL TRENDS

In Sproat Lake during 1999, seasonal patterns were opposite to those found in GCL. Sproat Lake densities and biomasses peaked in the spring (Figures 12 and 13) rather than in the fall, as was the case in GCL.

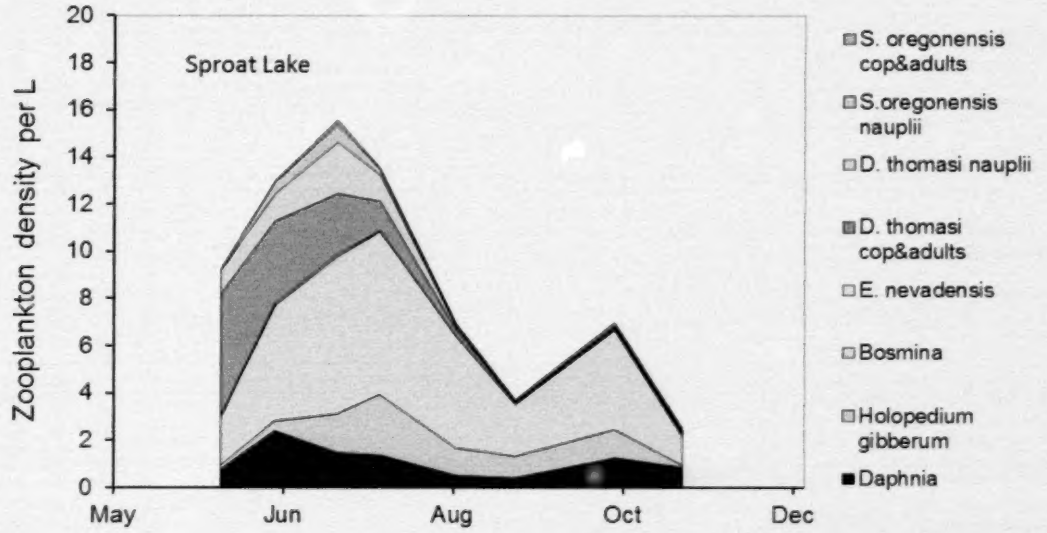

Figure 12. Sproat Lake 1999 zooplankton density per L. Details in Appendix 1.

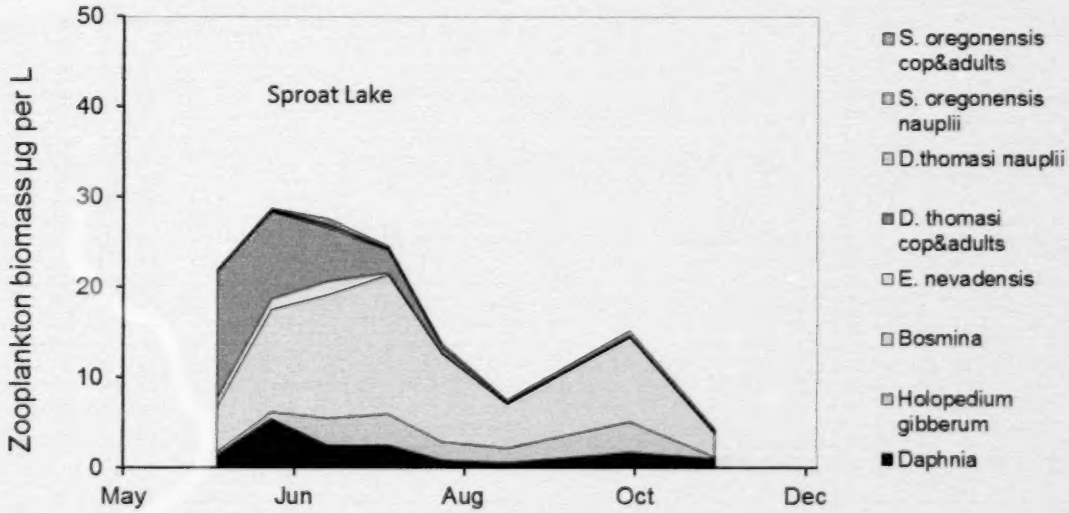

Figure 13. Sproat Lake 1999 zooplankton biomass µg L^{-1} dry weight. Details in Appendix 1.

ZOOPLANKTON PRODUCTION

Mean summer rates of production for the three species accounting for >95% of the Sproat Lake zooplankton biomass consumed by fish are summarized in Table 16. These rates are slightly higher than they were in fertilized GCL, despite the fact that during 1999, average GCL TP concentrations were similar to Sproat Lake TP concentrations and average GCL chlorophyll a concentrations were higher. In contrast with GCL's fall production peak, Sproat Lake zooplankton production (Figure 14) peaked in the spring.

Table 16. Average 1999 Sproat Lake (8 June – 18 November) zooplankton standing stock, egg density, and production.

Species	Summer average biomass $\mu g\ L^{-1}$ (dw)	Average egg density L^{-1}	Summer average production $\mu g\ L^{-1}\ d^{-1}$ (dw)	P/B per day	Summed P/B
Daphnia	2.028	0.281	0.062	0.031	5.0
Bosmina	9.000	0.482	0.233	0.026	4.2
D. thomasi	4.159	0.508	0.107	0.026	4.2

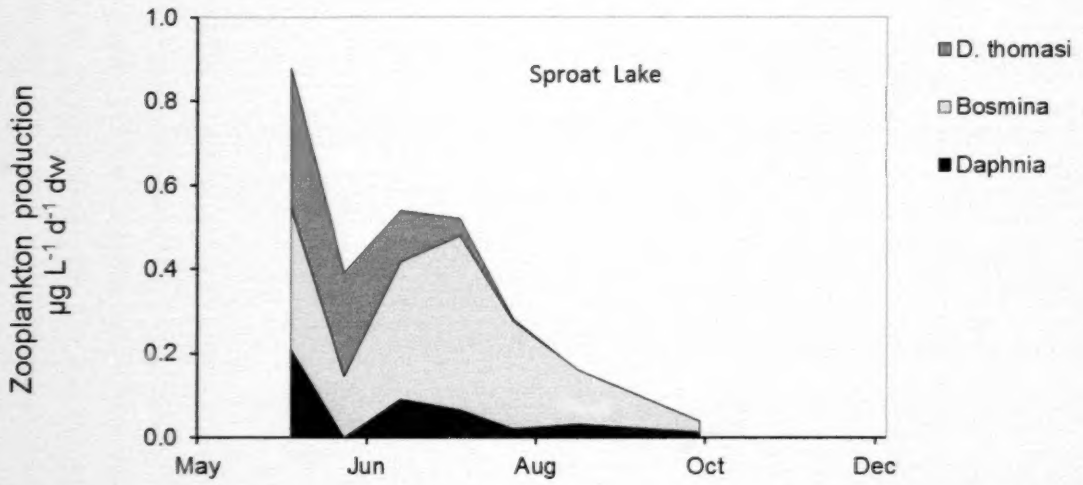

Figure 14. Average zooplankton production in Sproat Lake 1999.

SOCKEYE SALMON DENSITY, LENGTHS, AND WEIGHTS

1999 Sproat Lake juvenile sockeye salmon densities were close to their multi-year "average" (Table 17). For comparison, fall Sproat Lake densities based on the 10 years preceding 1999 (Hyatt and Rankin, unpublished observations), averaged 2481 ha^{-1} (maximum = 4970 ha^{-1}, minimum = 890 ha^{-1}).

Based on mean lengths (Table 18), 1999 Sproat Lake juvenile sockeye grew quickly in the spring and then slowed in the fall. Compared to weights averaged over the previous 10 years (Hyatt and Rankin, unpublished observations), juvenile sockeye grew slower than normal during 1999 (10 year fall Sproat Lake juvenile sockeye mean weight 3.8 g (min = 2.2 g, max = 4.8 g). The different patterns of seasonal growth observed for juvenile sockeye salmon in Sproat Lake and GCL reflect the patterns observed for zooplankton biomass and production. In GCL, both were higher in the fall and in Sproat Lake both were higher in the spring.

Table 17. Sproat Lake acoustic and trawl based estimates of abundance (virtually all limnetic fish sampled by trawl were juvenile sockeye salmon, although sticklebacks were occasionally encountered).

Survey Date	Pop. Est. (Total)	95% Con. Int.	Density per ha	95% CI per ha
27-Jun-99	5,385,927	1,582,467	1,426	419
19-Jul-99	7,140,529	1,789,456	1,891	474
30-Nov-99	8,461,797	983,370	2,240	260

Table 18. Sproat Lake 1999 trawl-based juvenile sockeye lengths and weights.

Survey Date	n	Mean length (mm)	Mean weight (g)	Stdev. length	Stdev. weight	95% CI length	95% CI weight
27-Jun-99	60	39.92	0.73	9.67	0.50	2.45	0.16
19-Jul-99	89	54.15	1.50	9.65	0.75	2.01	0.20
5-Aug-99	93	60.49	2.23	10.71	1.63	2.18	0.41
30-Nov-99	61	67.31	2.67	8.71	1.12	2.19	0.27

JUVENILE SOCKEYE DIETS

During the summer-fall of 1999, stomachs from 116 juvenile sockeye were examined. The most important prey included *Bosmina*, *D. thomasi* adults & copepodids, and adult

insects (dipterans). Mean weights (Table 19), used to convert crustacean zooplankton densities per fish stomach (Table 20) to weights per stomach (required for use in the bioenergetics model), were based on these field data.

Table 19. Mean weights (µg dry weight) for crustacean zooplankton, chironomids, and dipterans.

Daphnia	*Holopedium*	*Polyphemus*	*Bosmina*	*S. oregonensis* cop&adults	*Epischura*	*D. thomasi* cop&adults	Adult Dipterans	Chironomid larvae
1.69	1.89	3.8	2.20	3.92	10.03	2.13	50	11

Table 20. Rates of consumption of Sproat Lake prey by juvenile sockeye captured on four dates through the summer-fall of 1999. Mean weights (Table 19) were used to convert densities to biomasses.

Date	n	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	*S. oregonensis* cop&adults	*Epischura*	*D. thomasi* cop&adults	Adult Dipterans	Chironomid larvae
Average number of prey per fish stomach										
28-Jun-99	32	0.06	0.50	0.00	295.41	0.59	2.09	2.81	0.09	0.00
20-Jul-99	27	0.07	0.04	0.00	313.81	0.00	0.81	8.04	0.07	0.00
05-Aug-99	28	0.32	0.00	0.00	57.50	0.00	0.04	8.39	0.00	0.00
29-Nov-99	29	4.41	0.17	0.14	27.79	0.00	3.31	28.72	0.00	0.03
Average weight (µg dw) of prey per fish stomach										
28-Jun-99		0.1	0.9	0.0	651.2	2.3	21.0	6.0	4.7	0.0
20-Jul-99		0.1	0.1	0.0	691.7	0.0	8.2	17.1	3.7	0.0
05-Aug-99		0.5	0.0	0.0	126.7	0.0	0.4	17.9	0.0	0.0
29-Nov-99		7.5	0.3	0.5	61.3	0.0	33.2	61.2	0.0	0.4
Proportion by weight of prey per stomach										
28-Jun-99		0.000	0.001	0.000	0.949	0.003	0.031	0.009	0.007	0.000
20-Jul-99		0.000	0.000	0.000	0.959	0.000	0.011	0.024	0.005	0.000
05-Aug-99		0.004	0.000	0.000	0.871	0.000	0.002	0.123	0.000	0.000
29-Nov-99		0.045	0.002	0.003	0.373	0.000	0.202	0.372	0.000	0.002

NOCTURNAL DEPTH DISTRIBUTION OF SPROAT LAKE JUVENILE SOCKEYE SALMON

On two dates during 1999, we conducted acoustic surveys on the same transect (transect 7, Figure 4) approximately every half hour from near sunset to just after sun rise. The numbers in Table 21 represent percent of the total number of fish recorded during the sampling session (sundown to sunrise). As was the case in GCL, during the summer-to-fall interval, near sunset, fish began to appear from an area or depth of the lake that was outside the sampling transect, they aggregated between 5-20 m (shaded area) and then at sunrise, they disappeared from the sampling transect. During December, when the lake was much cooler and unstratified, the fish no longer exhibited a pronounced diel vertical migration, but rather remained relatively evenly dispersed between 5-30 m of water.

The aggregation depths brought the fish into contact with zooplankton that were associated with phytoplankton located in the euphotic zone. During August, the upper aggregation depths (5-10 m) exposed fish to temperatures ranging from 13-20 ^{O}C. The mean of 17 ^{O}C is thought to equal their thermal tolerance threshold. At GCL about 25% of the feeding fish were found in this warm epilimnetic zone, but at Sproat Lake only 14% of the fish targets were found in 5-10 m water depth (Table 21). Most were deeper (74% at10-20m) where temperatures of 7.8 -13.1 ^{O}C were well within their behavioural and physiological tolerance. By late November, the lake had destratified such that fish at all depths encountered temperatures well within their thermal tolerance range.

Table 21. Sproat Lake nocturnal depth distribution (% of total) of juvenile sockeye salmon. The shaded areas represent "concentration depths", defined as the depth distribution that includes >80% of the fish sampled during the night. Mean water temperatures are shown in blue (^{O}C) for 05 August and 01 December.

05 August 1999		Depth (m)							
Time In	Time Out	0-5	5-10	10-15	15-20	20-30	30-40	40-50	50-60
21:12	21:24	0	0	0	0	0	0	0	0
21:25	21:36	0	1	1	0	0	0	0	0
22:29	22:40	0	2	9	6	1	0	0	0
0:20	0:30	1	2	5	9	2	0	0	0
2:28	2:38	0	2	6	9	2	0	0	0
3:25	3:34	0	2	6	7	2	0	0	0
4:05	4:15	0	3	8	5	1	0	0	0
5:05	5:14	0	2	2	1	0	0	0	0
5:44	5:54	0	0	0	0	0	0	0	0
Mean water temperature		22	17	11	8	6	6	6	6
01 December 1999		Depth (m)							

Time In	Time Out	0-5	5-10	10-15	15-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	100-110
16:22	16:32	0	0	0	0	0	0	0	0	0	0	0	0	0
16:33	16:42	0	0	0	0	0	0	0	0	0	0	0	0	0
16:43	16:53	0	0	0	0	0	0	0	0	0	0	0	0	0
17:10	17:20	0	1	0	0	0	0	0	0	0	0	0	0	0
17:21	17:30	1	1	1	1	0	0	0	0	0	0	0	0	0
17:45	17:46	1	1	1	1	1	0	0	0	0	0	0	0	0
18:32	18:42	0	1	1	1	1	0	0	0	0	0	0	0	0
18:55	18:06	1	0	1	1	1	0	0	0	0	0	0	0	0
19:37	19:47	0	1	1	1	1	0	0	0	0	0	0	0	0
20:18	20:28	0	1	1	1	1	0	0	0	0	0	0	0	0
21:45	21:55	0	1	1	1	1	0	0	0	0	0	0	0	0
22:59	23:10	0	1	1	1	1	0	0	0	0	0	0	0	0
23:55	0:06	0	1	1	1	1	0	0	0	0	0	0	0	0
0:30	0:40	0	1	1	1	1	0	0	0	0	0	0	0	0
3:30	3:40	0	1	1	1	1	0	0	0	0	0	0	0	0
3:41	3:51	0	1	1	1	1	0	0	0	0	0	0	0	0
5:35	5:44	0	1	1	1	1	0	0	0	0	0	0	0	0
5:45	5:55	0	1	1	1	1	1	0	0	0	0	0	0	0
6:25	6:35	0	1	1	1	1	1	0	0	0	0	0	0	0
6:47	6:57	0	1	1	0	1	1	0	0	0	0	0	0	0
7:12	7:22	0	0	0	0	1	1	0	0	0	0	0	0	0
7:30	7:40	0	0	0	0	0	0	0	0	0	0	0	0	0
7:50	7:59	0	0	0	0	0	0	0	0	0	0	0	0	0
7:59	8:10	0	0	0	0	0	0	0	0	0	0	0	0	0
8:11	8:22	0	0	0	0	0	0	0	0	0	0	0	0	0
Mean water temperature		7	7	7	7	6	6	6	6	6	6	6	6	6

JUVENILE SOCKEYE BIOENERGETICS AND FOOD CONSUMPTION Simulations were run using the diet data described above (Table 20). Water temperatures were based on average temperatures between 5-30 m depth. Starting and ending mean weights were based on field data (Table 17 and 18). Model weights-at-age were compared with weights observed in the field and in order to achieve a reasonable fit between field and simulated mean fish weights-at-age, model parameters CB, CTO, and CTM in the model 3 consumption equation were adjusted to -1.4, 15 and 15 respectively, (Figure 15).

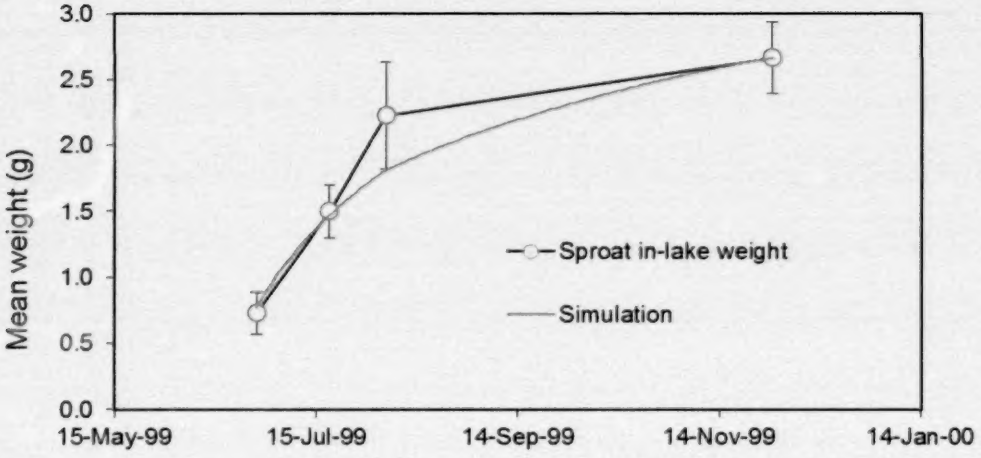

Figure 15. Sproat Lake field measured average weights (± 95% CI) of juvenile sockeye salmon and average weights simulated using the bioenergetics model.

The bioenergetics model estimates food consumption based on mean body weight changes observed in the field (0.73 g on 27 June at the beginning of the simulation and 2.67 g on 30 November at the end of a simulation period of 157 days). Model inputs also included daily water temperatures occupied by the fish and date-specific proportions (by weight) of each food type found in the guts of average fish (Table 20). Through an iterative process, the model estimates the amount of food the fish would have had to eat in order to grow as fast as it did grow in the field.

Figure 15 shows a substantial disagreement between field and simulated weights-at-age for 05 August 1999. On other dates the agreement was much better. Since curve fitting is strongly constrained by the structure of the model, the "fit" shown in Figure 16 represents our best approximation of food consumption in the field. The implication is that during the spring and fall, simulated food consumption accurately represents true food consumption in the field, but during midsummer, it seems likely that the model underestimates food consumption in the field.

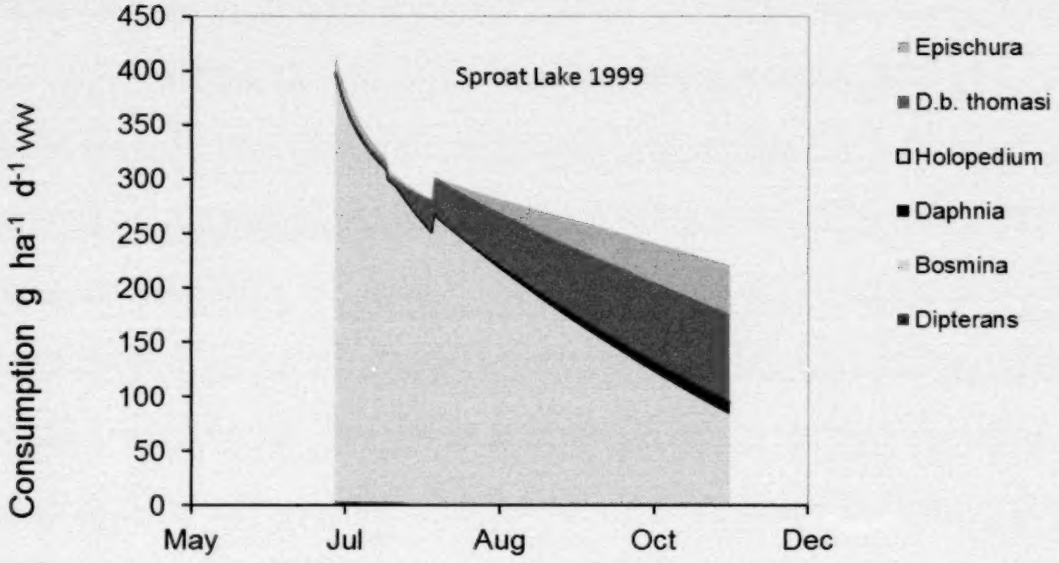

Figure 16. Bioenergetics-based estimates of Sproat Lake food consumption by juvenile sockeye salmon (g per ha wet weight per day) assuming that the fish fed between 5-30 m water depth.

In GCL, we saw that the highest zooplankton biomasses were reached in the fall and that most juvenile sockeye consumption and production was restricted to the fall time period. In Sproat Lake the opposite pattern was observed. In early June 1999, Sproat Lake sockeye were already three times larger than GCL sockeye and during June and July they grew at a very rapid rate, so that by the end of August they had achieved about 90% of their winter weight. Consequently, estimated rates of zooplankton consumption for Sproat Lake sockeye reflected that pattern. They were highest in the spring and declined through the season. This pattern was observed despite the fact that the modeled population of sockeye fry did not decline (no mortality – Table 17) and fall fish were larger than spring fish. Rather, the observed results were entirely driven by the very high spring growth rates that were observed both in the field and that we mimicked in the model.

In Sproat Lake, *Bosmina* was the most abundant prey consumed by weight followed by *D. thomasi* and *Epischura* (Figure 16). Note that the high spring rates of consumption of all three species were supported by high spring zooplankton biomasses (Figure 13). As the summer progressed, zooplankton biomasses declined and so did juvenile sockeye growth rates.

We may ask whether juvenile sockeye caused the observed decline in zooplankton biomass or whether an unrelated decline in zooplankton abundance resulted in reduced growth rates for Sproat Lake juvenile sockeye salmon. Using *Bosmina* as an example, the model predicted that on average through 1999, Sproat Lake juvenile sockeye consumed 203 g ha^{-1} d^{-1} wet weight of *Bosmina* (Figure 16). The average standing

stock biomass of *Bosmina* was 9.0 µg L^{-1} dry weight (Table 22) which converts to (2100*9) = 18,899 g ha^{-1} wet weight *Bosmina*. Therefore fish consumption averaged 1.1% per day of the *Bosmina* standing stock. Extending this analysis to other zooplankton, we have the results summarized in (Table 22).

Table 22. Average 1999 Sproat Lake rates of consumption by juvenile sockeye salmon.

Attribute	*Daphnia*	*Holopedium gibberum*	*Bosmina*	*S. oregonensis* cop & adults	*D. thomasi* cop & adults	*E. nevadensis*	Adult dipterans	Chironomid larvae
Mean biomass (µg L^{-1} dw)	2.0	1.8	9.0	0.3	4.2	0.5	nd	nd
Mean biomass g m^{-2} wet weight	0.4	0.4	1.9	0.1	0.9	0.1	nd	nd
Mean biomass g ha^{-1}	4260	3803	18899	578	8734	1125	nd	nd
Mean production g ha^{-1} d^{-1}	131	nd	489	nd	225	0	nd	nd
Consumption g ha^{-1} d^{-1}	4.6	0.0	203.1	0.0	49.0	19.7	0.7	0.0
% standing consumed d^{-1}	0.1	0.0	1.1	0.0	0.6	1.7	nd	nd
% production consumed d^{-1}	3.5	nd	41.6	nd	21.8	nd	nd	nd

Looking at this from the perspective of density and using *Bosmina* as an example, we know that on average all sockeye consumed 203 g ha^{-1} ww *Bosmina* per day. Therefore one fish consumed (203/2240) = 0.0906 g ww *Bosmina* per day. This is 90,625 µg ww d^{-1} which is 12,946 µg dw d^{-1}. One *Bosmina* had a weight of 2.2 µg dw. From this, we conclude that one fish consumed an average of 5885 *Bosmina* per day. Since average *Bosmina* density per L was 4.2 L^{-1}, each day one fish must have captured all of the *Bosmina* in 1401 L of water. Since one fish occupied 134 m^3 = 134,000 L of water, it must have consumed (1401/134,000) = 1.1% of the *Bosmina* population per day. This is the same result obtained above using weights. In all cases, zooplankton replacement rates (i .e. production) were always greater than average daily consumption, and average consumption by fish could not have accounted for observed declines in zooplankton.

However, when we compare seasonal daily rates of consumption by fish (Figure 16) with zooplankton densities (Figure 12), we see that during the spring, zooplankton biomasses were high and rates of consumption were higher than at any other time in the year. Comparisons of daily rates of consumption with zooplankton standing stocks and daily rates of production (Table 23) suggest that juvenile sockeye could have had relatively strong top-down impacts on *Bosmina* at all times in the year, and strong effects on *Daphnia* and *D. thomasi* during the fall. None of the rates suggests that fish could have caused declines in any of the populations, but given that the estimates do

not account for other sources of zooplankton mortality, we must conclude that during 1999 there was a relatively close balance between zooplankton production and consumption by fish.

Sproat Lake exhibited higher abundances of *Daphnia* than GCL in all samples and the greater inclusion of *Daphnia* in Sproat Lake sockeye diets (seasonal mean of 1.2% by weight for Sproat fish versus 0.2% by weight for GCL fish) is unsurprising. Similarly, the generally low abundance of *Daphnia* in both lakes relative to *Bosmina* explains the greater inclusion of the latter in diets for sockeye from both lakes. However, seasonal patterns of *Daphnia* consumption by fish were more puzzling. During the spring, Sproat Lake *Daphnia* densities were quite high (> 2 L^{-1}) (Figure 12), yet few or none appeared in fish stomachs. By contrast, Sproat fish consumed greater numbers of *Daphnia* coincident with lower *Daphnia* abundances in late summer (Table 23). From this we can only conclude that either *Daphnia* occupied habitat between spring to mid-summer which made them unavailable to fish or that they were ignored in favour of the far more abundant, but smaller *Bosmina*. The absence of dipterans from the diets of Sproat fish is also puzzling given that GCL sockeye diets contained significant quantities of adult dipterans that were most likely obtained during short forays into surface waters. These questions will only be answered by future studies linking diel migration by prey such as *Daphnia and Dipterans* with crepuscular and natural activity of sockeye fry.

Table 23. Percent of zooplankton standing stock and production consumed per day by juvenile sockeye.

	Daphnia		*Bosmina*		*D. thomasi*	
Sampling Date	% standing stock	% production	% standing stock	% production	% standing stock	% production
8-Jun-99	0.0	0.0	3.8	0.0	0.0	0.0
27-Jun-99	0.0	0.0	1.7	56.0	0.0	0.6
19-Jul-99	0.0	0.0	1.0	95.9	0.0	1.1
3-Aug-99	0.0	0.0	0.8	36.9	0.5	11.2
30-Aug-99	0.2	2.1	1.1	25.3	3.6	56.4
20-Sep-99	0.4	11.6	1.8	34.4	16.6	508.0
25-Oct-99	0.2	12.5	0.7	48.9	24.6	0.0
18-Nov-99	0.5	35.6	1.8	184.2	26.3	0.0

Finally, it should be noted that all of the indicators (TP, zooplankton biomass, juvenile sockeye fish biomass) show that during 1999, Sproat Lake was somewhat more productive than GCL even though Sproat Lake was not fertilized and GCL was fertilized. As noted earlier, Robinson and Barraclough (1972) showed that fertilization increased zooplankton standing stocks by about a factor of 10. From this we can conclude that Sproat Lake must have a much higher natural production capacity than untreated GCL. We can also conclude that suspension of fertilization in GCL would lead to substantial declines in zooplankton forage, sockeye growth rates, and possibly survival.

Although fertilization in GCL has been very successful, any consideration of fertilizer additions to Sproat Lake or termination of fertilizer additions at GCL should be approached with caution. There are two reasons. The first is that under treated conditions, GCL appears to roughly match the productivity of untreated Sproat Lake which, all other things being equal, means their two sockeye populations should exhibit similar smolt production and be capable of withstanding equivalent exploitation rates on returning adults. Actions that threaten this between population production parity could well complicate their management for sustainable yield to the Barkley Sound mixed stock fishery. In addition to this concern, Sproat Lake algal communities are sporadically dominated by two diatoms (*Rhizosolenia eriensis* now *Urosolenia eriensis* and *Rhizosolenia longiseta* now *Urosolenia longiseta*) that are much too large to be consumed by zooplankton. Further, there is some risk that fertilizer additions might result in inordinate production by these taxa such that little benefit from fertilization would accrue to either zooplankton or juvenile sockeye production. Consequently, any serious consideration of future fertilization of Sproat Lake would need to be informed by several years of detailed data collection, including genus-specific phytoplankton data.

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APPENDIX 1: ZOOPLANKTON DENSITY AND BIOMASS

Table 1. Year 1999 Great Central Lake and Sproat Lake zooplankton (a) density (per L) and, (b) biomass (per L dry weight).

(a)	Density per L							
Sampling Date	*Daphnia*	*Holopedium gibberum*	*Bosmina*	*S. oregonensis* cop & adults	*S. oregonensis* nauplii	*D. thomasi* cop & adults	*D. thomasi* nauplii	*E. nevadensis*
Great Central Lake								
3-Jun-99	0.01	0.00	0.24	0.07	0.05	2.90	0.07	0.02
22-Jun-99	0.01	0.00	1.11	0.11	0.13	3.01	0.13	0.06
12-Jul-99	0.02	0.00	2.56	0.01	0.48	1.49	0.43	0.00
2-Aug-99	0.02	0.03	2.85	0.01	0.59	2.60	0.83	0.00
21-Aug-99	0.02	0.08	1.52	0.04	0.61	1.75	0.62	0.00
13-Sep-99	0.02	2.05	3.69	0.26	1.66	3.92	1.34	0.00
26-Oct-99	0.02	1.98	13.70	0.31	0.01	0.39	0.01	0.00
25-Nov-99	0.02	0.47	5.81	0.26	0.04	0.25	0.04	0.00
Sproat Lake								
8-Jun-99	0.77	0.17	2.05	0.01	0.02	5.15	0.99	0.07
27-Jun-99	2.40	0.40	4.88	0.03	0.51	3.49	1.15	0.10
19-Jul-99	1.47	1.63	6.66	0.16	0.77	2.56	2.18	0.12
3-Aug-99	1.38	2.54	6.91	0.05	0.22	1.25	1.12	0.03
30-Aug-99	0.51	1.15	4.72	0.08	0.05	0.28	0.13	0.02
20-Sep-99	0.41	0.90	2.21	0.07	0.00	0.09	0.01	0.01
25-Oct-99	1.26	1.18	4.22	0.12	0.03	0.09	0.05	0.01
18-Nov-99	0.86	0.08	1.23	0.10	0.08	0.09	0.05	0.02

(b)	Biomass per L dw							
Sampling Date	*Daphnia*	*Holopedium gibberum*	*Bosmina*	*S. oregonensis* cop & adults	*S. oregonensis* nauplii	*D. thomasi* cop & adults	*D. thomasi* nauplii	*E. nevadensis*
Great Central Lake								
3-Jun-99	0.01	0.00	0.41	0.17	0.02	5.50	0.02	0.11
22-Jun-99	0.02	0.01	1.61	0.35	0.03	7.79	0.03	0.43
12-Jul-99	0.06	0.00	2.93	0.04	0.10	2.89	0.08	0.00
2-Aug-99	0.04	0.05	3.93	0.03	0.13	2.56	0.15	0.03
21-Aug-99	0.04	0.13	2.19	0.21	0.12	1.46	0.10	0.00
13-Sep-99	0.02	2.94	6.96	0.92	0.38	4.10	0.22	0.08
26-Oct-99	0.07	7.43	35.30	1.02	0.00	0.70	0.00	0.05
25-Nov-99	0.04	1.96	13.93	1.16	0.01	0.55	0.01	0.00
Sproat Lake								
8-Jun-99	1.45	0.33	4.99	0.04	0.00	14.04	0.15	0.97
27-Jun-99	5.44	0.72	11.35	0.08	0.10	9.70	0.14	1.17
19-Jul-99	2.49	2.98	13.67	0.56	0.18	5.87	0.28	1.53
3-Aug-99	2.55	3.41	15.39	0.22	0.04	2.57	0.15	0.22
30-Aug-99	0.89	1.98	9.75	0.35	0.01	0.65	0.02	0.14
20-Sep-99	0.61	1.56	4.91	0.19	0.00	0.17	0.00	0.07
25-Oct-99	1.74	3.34	9.38	0.46	0.01	0.14	0.01	0.08
18-Nov-99	1.07	0.16	2.56	0.31	0.02	0.14	0.01	0.11